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A Simulation Model for Growth of the Submersed Aquatic Macrophyte Sago Pondweed (*Potamogeton pectinatus* L.)

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Final report

ABSTRACT: A simulation model for biomass dynamics of the submersed macrophyte *Potamogeton pectinatus* L. is presented. The model (POTAM) is based on carbon flow through the vegetation in meter-squared (m^2) water columns. It includes descriptions of several factors that affect biomass dynamics, such as site characteristic changes in climate, temperature, water transparency, water level, pH, and oxygen effects on CO_2 assimilation rate at light saturation, wintering strategies, mechanical control (removal of shoot biomass), and grazing. The characteristics of community and site can be easily modified by the user.

POTAM incorporates insight into the processes affecting the dynamics of a sago pondweed community in relatively shallow, hard water (0.1- to 6-m depth; dissolved inorganic carbon concentration > 0.8 mmol and pH > 6), under ample supply of nitrogen and phosphorus in a pest-, disease-, and competitor-free environment under the prevailing weather conditions. It has been calibrated on data pertaining to a sago pondweed community in the Western Canal near Zandvoort, The Netherlands. At this site, growth starts from the subterranean tubers alone. Plant biomass usually peaks once a year, in July, and intensive downward transport of soluble carbohydrates occurs after anthesis, used for the formation of tubers that grow into the sediment.

POTAM simulated the dynamics of plant and tuber biomass and tuber numbers in the Western Canal near Zandvoort, The Netherlands, well over a period of 1 to 5 years. Starting from measured instead of nominal tuber size increased the similarity between simulated and measured plant data. The importance of several plant species-characteristic properties was explored, namely, of leaf surface:dry weight ratio, tuber bank density, anchorage depth, and presence/absence of wintering shoots.

The model has been used to calculate plant and tuber biomass and tuber numbers for other sites as well. In Lake Veluwe, The Netherlands, a site with a temperate climate, simulated plant biomass and newly produced tuber densities were similar to measured ones in two consecutive years, but timing in the simulated plants was delayed the second year. In the Byrnes Canal, California, with a far warmer temperate climate, simulated plant biomass and tuber bank density were similar to measured values when a lower self-shading coefficient than the nominal one and the same tuber size/tuber number per plant as measured were used. However, plant biomass and tuber bank density were lower with the nominal self-shading coefficient. In the tropical Lake Ramgarh, India, a simulated peak plant biomass similar to measured was found using the same lower self-shading coefficient as run for the California site, and almost no tubers were formed. Verification of simulated with measured tuber numbers was not possible, since tubers had not been measured.

Several case studies are presented in which POTAM generated insight useful for management aimed at conserving or controlling sago pondweed populations. The model was used to calculate the tentative effects on sago pondweed populations of (a) water level fluctuations, including floods and droughts, in the Upper Mississippi River; and (b) plant and tuber mass removal by cutting or grazing.

Sensitivity analysis showed that maximum plant biomass is most sensitive to a change in photosynthetic activity at light saturation but not to a change in light use efficiency. Maximum plant biomass was also strongly affected by changes in pre-anthesis development rate. End-of-year tuber number was sensitive to 7 out of the 9 parameters tested. Sensitivity was greatest to changes in pre-anthesis development rate.

Effects of changes in environmental factors were analyzed by applying the same method as used for sensitivity analysis. Maximum plant biomass and end-of-year tuber number proved to be sensitive to changes in climate.

The model can be used as a tool to predict the dynamics of a sago pondweed community over 1- to 5-year periods. Running the model with different parameter values specific for any particular site and/or treatment helps in gaining insight into the predominant mechanisms regulating submersed plant dynamics.

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Preface

1 Introduction

Background

The extent to which aquatic macrophytes influence the ecosystem is proportional to plant mass and depends on plant species and physicochemical factors. Therefore, predictions of the environmental impact of management measures on aquatic plant communities should be based on accurate estimates of (a) plant species, mass, and pertinent physiological properties, (b) the contribution of the plant to the various food chains, and (c) the contribution of the decay of the plant to biogeochemical cycling and oxygen regime. A simulation model that simulates metabolism and growth of a specific aquatic macrophyte community may serve as a useful tool in this respect.

Although the number of simulation models for growth of monotypic, submersed macrophyte communities is increasing (e.g., Titus et al. 1975; Best 1981; Collins and Wlosinski 1985; Best and Jacobs 1990; Hootsmans 1991; Scheffer et al. 1993; Best and Boyd 1996, 1999, 2001), it is still relatively low compared to that for terrestrial vegetation. The current model has been developed because none of the existing models was suitable to simulate the behavior of a monotypic sago pondweed community under various environmental and climatological conditions over a period ranging from one season to several years.

Taxonomy and Distribution of Sago Pondweed within the United States

The submersed, rooted aquatic macrophyte sago pondweed or *Stukenia pectinata* belongs to the monocotyledonous family of Stukeniaceae. This species has recently moved from the Potamogetonaceae (Voss 1972; Godfrey and Wooten 1997) into the Stukeniaceae (Crow and Hellquist 2000). This report uses the taxonomic name commonly cited up to 2000, since all literature pertains to the formerly used name of *Potamogeton pectinatus* for this plant. The name *Potamogeton* is derived from the Greek word for "river neighbor," and the epithet *pectinatus*, "comb-like," is derived from the closely set insertion of the frequently branched stem and narrow filiform leaves of the plant, which give it a bushy appearance. The following synonyms have been used in North America: *P. interruptus* Kit, *P. latifolius* J. Robbins, *P. flabellatus* Bab., and *P. columbianus* Suksdorf. Many other synonyms have been used in Europe. Earlier the genus was

considered as a part of the families of the Zosteraceae and Najadaceae (Fernald 1950). Forty *Potamogeton* species have been documented relatively recently in North America by Kartesz and Kartesz (1980), and 35 *Potamogeton* species by the U.S. Department of Agriculture (1982). Approximately 100 *Potamogeton* species have been identified worldwide (Kadono 1982). *P. pectinatus* has an average of 2n=78 chromosomes (Kalkman and Van Wijk 1984). It is genetically heterogeneous (Hettiararchi and Triest 1986; Van Wijk et al. 1988) and hybridizes with *Potamogeton filiformis* and *P. vaginatus* (Hagstrom 1916; Dandy and Taylor 1946; Harrison 1949). Differences in morphology and ecological characteristics have been linked to annual and perennial *P. pectinatus* ecotypes (Van Wijk 1983). Two varieties have been associated with differences in water quality: the variety *scoparius* with bicarbonate-poor waters and the variety *interruptus* with sewage-polluted waters (Wiegleb 1978).

Sago pondweed occurs in fresh alkaline to slightly saline water (Den Hartog 1981) with a high alkalinity and pH > 6 (Lohammar 1938; Spence and Maberly 1984), at depths of 0.1 to 7 m, and rooted in sediment types varying from bedrock to mineral bottoms with particles sizes ranging from rubble to fine clay (Wong and Clark 1976; Pip 1987). In contemporary floras (Fernald 1950; Gleason 1968), *P. pectinatus* is cited in the American continent from Quebec and Newfoundland to Alaska, in the eastern half of the United States, southwestward to Arizona, and southward to South America. It is native to the western United States and was probably introduced into Florida. Its occurrence has been documented also in Western Europe (Van Wijk 1988), the Russian Federation (Lapirov and Petukhova 1985), and in subtropical and tropical areas, such as India (Sahai and Sinha 1973). It is sometimes considered a nuisance plant in areas with a warm climate, where by virtue of its prolific growth and reproduction, it may interfere with human utilization of freshwater resources, become aesthetically displeasing, or displace desirable indigenous vegetation. However, data on total biomass and productivity indicate that they are small compared with those of several terrestrial plant communities (Spencer and Bowes 1990). This apparent anomaly may be due largely to the uneven distribution of biomass over the water column, with typically > 60 percent concentrated in the upper water layers (canopy formation). The tubers and seeds have been planted in many localities to improve habitat for ducks. The entire plant is relished by waterfowl. It also provides good habitat for fish. These plantings probably have extended the distribution of this plant beyond its natural range (Martin et al. 1951). A comprehensive review of English literature on *P. pectinatus* has been published by Kantrud (1990).

The simulation model developed in this study concerns sago pondweed. The following appendices are included in this report: model listing (Appendix A), variable listing (Appendix B), and a discussion of manipulation of literature data used for the model equations (Appendix C). A user's manual is published in Best and Boyd (in preparation).

2 POTAM: Description of Model

Modeling Concepts

The POTAM (Version 1.0) model simulates growth of a typical monoecious sago pondweed community. In the model, growth is considered to be the plant dry matter accumulation, including subterranean tubers, under ample supply of nitrogen and phosphorus, in a pest-, disease-, and competitor-free environment under the prevailing weather conditions. At least one plant cohort waxes and wanes per season in different climatological regions, varying from temperate to tropical. The rate of dry matter accumulation is a function of irradiance, temperature, CO_2 availability, and plant characteristics. The rate of CO_2 assimilation (photosynthesis) of the plant community depends on the radiant energy absorbed by the canopy, which is a function of incoming radiation, reflection at the water surface, attenuation by the water column, attenuation by the plant material, and leaf area of the community. From the absorbed radiation, the photosynthetic characteristics of individual shoot tips, and the pH-determined CO_2 availability, the daily rate of gross CO_2 assimilation of the community is calculated. These calculations are executed in a set of subroutines added to the model.

Part of the carbohydrates produced is used to maintain the existing biomass. The remaining carbohydrates are converted into structural dry matter (plant organs). In the process of conversion, part of the weight is lost in respiration. The dry matter produced is partitioned among the various plant organs using partitioning factors defined as a function of the phenological cycle of the community. The dry weights of the plant organs are obtained by integration of their growth rates over time. The plant winters through tubers in the sediment without or with biomass present. All calculations are performed on a square meter basis. Since environmental factors and plant growth characteristics vary with depth, the water column and associated growth-related processes have been partitioned in 0.10-m depth classes in the model (Titus et al. 1975).

Seed formation has not been included in the model, because its role in maintaining an existing sago pondweed community at the same location in relatively shallow waters is believed to be minimal (Van Vierssen and Verhoeven 1983) and investment in terms of carbon allocation low (Doyle 2000). Dispersal and colonization of new habitats by seeds and axillary turions are recognized as

important characteristics of sago pondweed (Yeo 1965; Kantrud 1990). The latter processes, however, are better described using other modeling approaches (based on logistic regression or on descriptions of population dynamics varying in time and in space), as discussed by Scheffer (1991).

POTAM requires as input physiological properties of the plant community (in this case of sago pondweed) and actual environmental and weather conditions at the site characterized by geographical longitude and latitude, i.e., height of the water column, water temperatures (optional), alkalinity, pH, day length, daily maximum and minimum temperatures, and irradiance for each day of the year. It can be run for periods of 1 to 5 years.

Modeling Approach

POTAM is a mechanistic model that explains plant growth on the basis of the underlying processes, such as CO_2 assimilation and respiration, as influenced by environmental conditions. This type of model follows the state-variable approach in that it is based on the assumption that the state of each system can be quantified at any moment and that changes in the state can be described by mathematical equations. In this type of model, state, rate, and driving variables are distinguished. State variables are quantities such as biomass and number of individuals of a population. Driving variables characterize the effect of environment on the system at its boundaries, such as climate and food supply. Each state variable is associated with rate variables that characterize its rate of change at a certain instant, as a result of specific processes. These variables represent flows of material between state variables, the values of which are calculated from the state and driving variables according to knowledge of the physical, chemical, and biological processes involved. After the values of all rate variables are calculated, they are then used to calculate the state variables according to the scheme: state variable at time $t + \Delta t$ equals state variable at time t plus the rate at time t multiplied by Δt. This procedure, called numerical integration, gives the new values of the state variables, from which the calculation of rate variables is repeated. To avoid instabilities, the time interval Δt must be small enough so that the rates do not change materially within this period. This is generally the case when the time interval of integration is smaller than one-tenth of the "time coefficient" or "response time." This characteristic time of a system is equal to the inverse of the most rapid relative rate of change of one of its state variables. The smaller the time coefficient, the smaller the time interval of integration (Rabbinge and De Wit 1989).

The predictive ability of mechanistic models does not always live up to expectations. It should be realized, however, that each parameter estimate and process formulation has its own uncertainty, and that uncertainties in parameter estimates may accumulate in the prediction of the final yield. The primary aim of this model is to increase insight into the system studied by quantitatively integrating the current knowledge in a dynamic simulation model. By studying the behavior of such a model, better insight in the real system is gained.

Implementation

The POTAM model was implemented as a FORTRAN77 program. For numerical integration, the Runge-Kutta technique is used, which allows employing a variable time-step. The program, as it is being run, integrates the equations once per day in the main subroutine MODEL (Figure 1); once per second in the subroutines calculating day length and instantaneous irradiance (ASTRO) and instantaneous gross assimilation (ASSIM); and three times per day in the subroutine calculating daily total gross assimilation (TOTASS; Gaussian integration). Instantaneous gross assimilation is calculated per second and converted to hourly rates within ASSIM.

Model approach and organization are similar to those used for agricultural crops (SUCROS1, Goudriaan et al. 1992). Several features of a generic growth model for submersed angiosperms (SUBANG, Best and Jacobs 1990), and for other submersed plant species (HYDRIL, Best and Boyd 1996; MILFO, Best and Boyd 1999; VALLA, Best and Boyd 2001) have been used.

POTAM runs within a FORTRAN Simulation Environment (FSE) shell, Version 2.1, to enable easy handling of input and output files and rapid visualization of the simulation results (Van Kraalingen 1995). It can be executed on most PCs as a stand-alone version, but it requires the use of DOS. Because of its language and simple structure, it will generally be compatible with ecosystem models that accept FORTRAN. Switching from a WINDOWS-based to a DOS-based system may be accomplished through the WINDOWS Start menu, by activating the **Run** option and typing **CMD**, then **Enter**.

The organization of the model and its subroutines in combination with the FSE shell is illustrated in Figure 1.

Model Features

Features of POTAM are as follows:

a. Phenology is tied indirectly to temperature through development rate, and is, therefore, independent of day of year; thus, the model can be used under climatological conditions ranging from temperate to tropical.

b. Plant growth starts from the subterranean tuber bank alone, which may range from tuber densities as low as one to a tuber bank with wintering plants present.

c. One or more plant cohorts can be active in temperate as well as tropical climates; in case of plantlet death during prolonged periods of negative net photosynthesis early in the season, the dead plant cohort is succeeded by the next sprouting plant cohort.

MAIN

* Displays model header

* Calls FSE

* END

FSE
driver

(Fortran Simulation
Environment)

version 2.1

subroutine
MODELS

* Interface FSE-driver
and
simulation model

subroutine
MODEL
Declaration of:
- Formal parameters
  (shell terms)
- Model parameters etc.
- Calculations
- Calls to subroutines

subroutine
ASTRO

* Photoperiod

* Daylength

* Irradiation

subroutine
TOTASS

* Daily total gross
  assimilation
  (3-point Gaussian
  integration)

subroutine
ASSIM

* Light attenuation
  water + vegetation

* Instantaneous
  gross assimilation
  (0.1 m depth layers)

Figure 1.   Relational diagram illustrating the organization of the model POTAM
and its subroutines in combination with the FSE shell

d.   Photosynthetic response is to instantaneous irradiance.

e.   Air or water temperatures must be used to run the model. When air
temperatures are used, the lag period between air temperature and
(calculated) water temperatures can be varied between 1 and 7 days; this
is an important feature for application in water bodies varying in depth,
with large groundwater inputs, etc.

f. The model can be used for communities at water depths that may vary between years and daily within the year, with depths ranging from 0.1 to 6.0 m; this is an important feature for application in reservoirs and rivers.

g. Plant parameter values and climatological variables can be easily changed.

h. Effects of removal of plant biomass through cutting and of tubers through grazing can be calculated if desired.

3   Model Processes

Morphology, Phenological Cycle, and Development

Morphology and phenological cycle of sago pondweed

Pondweeds are perennial submersed aquatic macrophytes that may regenerate from rhizomes, tubers, turions (detached winterbuds), or seeds. Because of its multiple regenerative strategies, stress tolerance, and competitive ability, which enable the plant to occupy mechanically disturbed areas, *P. pectinatus* is considered as a ruderal (Grime 1979; Kautsky 1987).

The monoecious *P. pectinatus* is a rooted submersed macrophyte, with a slender growth form composed by long stems with narrow, mostly filiform, leaves and emergent inflorescenses. In some populations long shoots are formed and branching is strongest at the end of the shoots. Luxuriant growth may lead to densely packed leaves, branches, and inflorescences in the upper part of the water column, with vegetation density increasing close to or on the water surface as water levels decrease. Other populations produce shorter shoots, and branching starts soon after the development of shoots (Den Hartog 1982). In the latter case, plant biomass is divided over the entire water column. Shoot length and branching appear to be characteristic of certain populations, but are also influenced by environmental conditions such as light (Van Wijk et al. 1988), current velocity, and nutrient availability (Van Wijk 1986; Vermaat and Hootsmans 1994a). In shallow waters, sago pondweed usually behaves as an annual, because it is sensitive to frost, like most submersed macrophytes, and decomposes rapidly in water (Lohammar 1938; Lapirov and Petukhova 1985). However, in deeper waters, green perennial sago pondweed shoots can be found (Hammer and Heseltine 1988). Flowering occurs once a year, from late June to August in the Northern Hemisphere (Yeo 1965). In mild climates, flowering may extend up to 5 months (Gupta 1968; Ramirez and San Martin 1984). Flowering usually coincides with peak biomass and is followed immediately by sloughing. The inflorescenses are bisexual spikelets on axillary peduncles, consisting of four staminate flowers surrounded by four pistillate ones (Uhl 1947). The production of viable seeds requires pollination on the water surface by buoyant pollen originating from a different specimen than the sago pondweed parent plant. Fruits mature under water (Mason 1969; Philbrick and Anderson 1987). The fruit of sago pondweed is a greenish, plump nutlet 2.5-5 mm wide. Other, perennial diaspores are subterranean tubers formed on the stolons within the sediment and

axillary turions. Both tubers and turions are composed of a small amount of dividing tissue surrounded by several fleshy leaves. The parent plants senesce and disintegrate at the end of the growth season, and the tubers and turions hibernate within and/or on top of the sediment until their emergence the following spring, which completes the annual growth cycle. Tubers are depleted and disintegrate following the summer in which they were formed. Turions are smaller and are depleted earlier than tubers.

The plants may form numerous perennial diaspores, tubers and turions, and/or annual seeds. For example, in a single-season culture experiment, Yeo (1965) grew 36,000 subterranean tubers, 800 axillary turions, and 6,000 drupelets from one single turion, and 63,000 drupelets and 15,000 subterranean tubers from one single drupelet.

Tubers are considered the main propagules of sago pondweed in shallow waters because the fruitlike seeds, or drupelets, require stratification to germinate well in a temperate climate and lose their viability in deep waters and by burial within the sediment (Haag 1983), and because the species does not compete successfully with other seed-producing shallow-water species (Van Vierssen and Verhoeven 1983). Relatively small tubers and turions may survive drawdown conditions (Spencer 1987), but are usually sensitive to desiccation with sprouting being reduced by > 80 percent in tubers after drying for 64 hours and turions being more sensitive than tubers (Basiouny et al. 1978). However, sago pondweed tubers exposed to desiccation treatments within the sediment up to 15 months proved to retain up to 30 percent of their sprouting potential in fresh water and up to 60 percent in brackish systems (Van Wijk 1989). Consequently, it is believed that sago pondweed may survive drawdown in a temperate climate only in the form of large tubers in the upper sediment layer.

Seeds may be important in long-distance dispersal and as insurance against local extinction. This is supported by the observations that (a) seed germination is enhanced by passage through duck guts up to a duration of 44 hours (Guppy 1897; Ridley 1930; De Vlaming and Proctor 1968), (b) in several established wetlands almost all sago drupelets were recovered close to the shore (Pederson and Van der Valk 1984), and (c) seedlings germinated from drupelets have seldom been observed (Van Wijk 1983, 1988).

Description of development and phenological cycle in POTAM

The phenology of a plant community, for which the development phase can be used as a measure, quantifies physiological age and is related to its morphological appearance. The development phase cannot be expressed simply as chronological age, because several environmental factors such as temperature and stress (e.g., nutrients, grazing) can speed up or reduce the rate of phenological development. Contrary to what is suggested by intuition, the rate of plant growth per se has no effect on phenological development, as long as the growth rate is not very low (Penning de Vries et al. 1989b, and citations therein). The concept of development phase is used to characterize the whole plant community; it is not appropriate for individual organs.

Development phase (DVS) is a state variable in POTAM. DVS is dimensionless, and its value increases gradually within a growing season. The **development rate** (DVR) has the dimension d^{-1}. The multiple of rate and time period yields an increment in phase.

The response of developmental rate to temperature in the current model is in accordance with the degree-day hypothesis (Thornley and Johnson 1990a). The idea is as follows. The mean temperature $\overline{T_i}$ (°C) for each day i is measured, and a sum h (degree-day sum, °C) is formed according to the following equation:

$$h = \sum_{i=1}^{j}\left(\overline{T_i} - T_c\right)$$

(1)

which includes only those terms where $\overline{T_i}$ is above some threshold value T_c. When h reaches a particular value, this signifies that a phase in development is complete, and this is generally associated with a biological event that occurs over a short period of time and is readily observed. The day-degree sum h essentially integrates some underlying temperature-dependent processes. For sago pondweed, for example, there are various phases in the development of the plant, and the temperature sum is found to have a certain value for the successful completion of each. The temperature threshold T_c may be different for each of these phases. The approach is based on the notion of a developmental rate whose response to temperature is approximately linear over a restricted temperature range. Comparison with actual temperature responses found in agricultural crops suggests that this is not unreasonable, and the method works well in practice. It is implicitly assumed that the organism possesses a developmental clock that is proceeding at the rate k_d (development rate, d^{-1}). In general, it is to be expected that the development rate k_d may depend on a number of quantities. This can be represented by the following equation:

$$k_d = f(V, P, E)$$

(2)

in which f represents some function of the state variables V, parameters P, and environmental quantities E. The temperature-sum rule works because the most important environmental variable is temperature, and the response to temperature is approximately linear.

The phenological cycle is described using sago pondweed in the Western Canal near Zandvoort, The Netherlands, 1987 (Appendix C), and climatological data from De Bilt, The Netherlands, 1987.

In the model, the temperature affecting development of sago pondweed can be chosen as equal to the daily average air temperature at the height of the growing point of the shoots, with a user-defined lag period to correct for deviations in temperature of the water body in which the aquatic community grows compared with air temperatures (7 days is nominal). It is more accurate to use water temperatures for this purpose, but since water temperatures are not always

available for the site for which the user wants to run the model, POTAM can be run using either one.

Temperature can have a different effect on the rate of phenological development in the vegetative phase and in the reproductive phase. These differences indicate that the physiological process of development may not be the same before and after anthesis. Only one flowering period occurs in a temperate climate, i.e., from the end of June to August (Appendix C). Flowering behavior in a tropical climate is presumed to be similar to that in a temperate climate (Sahai and Sinha 1973).

The following DVRs were derived from the Western Canal field data (Appendix C): 0.015 d^{-1} prior to the flowering period (**DVRVT**), and 0.040 d^{-1} subsequently (**DVRRT**), at a reference temperature of 20 °C and a temperature threshold of 3 °C. These development rates are considered as typical for temperate regions. They are in the same order of magnitude as those found for the other submersed hydrilla (*Hydrilla verticillata* (L.F.) Royle), Eurasian watermilfoil (*Myriophyllum spicatum* L.), and American wildcelery (*Vallisneria americana* Michx.) (Best and Boyd 1996, 1999, 2001), but higher than that found for the terrestrial, tuber-forming, sweet potato (development rate of 0.006 d^{-1} at a reference temperature of 27 °C; Kooman 1995). For sago pondweed populations in the tropics, the same development rates and timings as in temperate regions were applicable (Sahai and Sinha 1973).

DVS has the value 0.0 when the simulation starts at the first Julian day number (Table 1). The simulation starts using an observed tuber bank density, with a certain, chosen (this chapter, section, "Wintering and Sprouting of Tuber Bank") individual tuber weight as initial values. The quantities of leaves, stems, and roots are set equal to 0. If simulation of a sago pondweed community at another site is desired, the simulation can start also with wintering plants present; first, however, initial quantities of plant organs must be calculated.

For a sago pondweed community in a temperate climate, the sprouting of the tubers, i.e., the initiation of growth activity, occurs at DVS 0.211. Sprouts of the first plant cohort develop through remobilization of carbohydrates from the tubers. The sprouts elongate rapidly up to the water surface, and subsequently follow a typical umbrella-shaped spatial distribution within the water column. Anthesis is initiated at DVS 1.000 and finishes at DVS 2.000, just before new tubers are initiated. Tubers can be formed directly when initiated, in contrast to hydrilla where tuber formation lags behind tuber initiation (Best and Boyd 1996). Tuber formation, downward translocation, and senescence set in at DVS 2.001 and continue until the end of the year (Table 1).

Sago pondweed plants in tropical regions behave similarly in terms of DVS to those in temperate regions, except that tropical plants require on average a 1.6 times higher 3 °C-day-degree sum to complete their individual life cycle than temperate cohorts.

**Table 1
Relationship between DVS of Sago Pondweed, Day of Year and
3 °C Day-Degree Sum in a Temperate Climate (DVR Prior to
Flowering Period, DVRVT= 0.015; DVR from Flowering Period
Onward, DVRRT= 0.040)**

| Developmental Phase | | Day Number | 3 °C Day-Degree Sum |
Description	DVS value		
First Julian day number → tuber sprouting and initiation elongation	0 = 0.210	0 = 77	1 = 193
Tuber sprouting and initial elongation → leaf expansion	0.211 = 0.929	78 = 187	194 = 1301
Leaf expansion → floral initiation and anthesis	0.930 = 1.000	188 = 195	1302 = 1434
Floral initiation and anthesis → induction of tuber formation, tuber formation and senescence	1.001 = 2.000	196 = 233	1435 = 2077
Tuber formation and senescence → senesced	2.001 = 4.033	234 = 365	2078 = 3193
Senesced	4.033	365	3193

Note: Calibration was on field data on biomass and water transparency from the Western Canal near Zandvoort, The Netherlands, 1987 (Appendix C) and climatological data from De Bilt, The Netherlands, 1987.

Maximum Biomass and Plant Density

Seasonal biomass maxima can vary considerably over time and space. In both temperate and tropical climates usually one biomass peak per growth season was found, which occurred just before flowering. The highest standing crop of sago pondweed is found in saline and brackish lakes. In the temperate saline Swartvlei, between Port Elizabeth and Cape Town in South Africa (longitude 22°46' E, latitude 34° S) 1,952 g dry weight (DW) m^{-2} was measured by Howard-Williams (1978); in Lake Mariut, Egypt (longitude 30°10' E, latitude 31°10' N), 1,568 g DW m^{-2} by Aleem and Samaan (1969); and in a brackish pool near Yerseke, The Netherlands (longitude 3°36' E, latitude 51°30' N), 1,312.5 g DW m^{-2} was found by Van Wijk et al. (1988). A somewhat lower maximum plant biomass of 712 g DW m^{-2} has been recorded for fresh water in Badfish Creek, WI, USA (approximate longitude 89°22' W, latitude 43°4' N), by Madsen and Adams (1988). Far lower biomass values are usually found under stressed conditions, such as caused by turbidity due to eutrophication and/or resuspension in shallow freshwater lakes in Poland (Ozimek et al. 1986), notably 5 to 112 g DW m^{-2}, or exposure to high waves in the shallow Baltic Sea, Sweden (longitude 14°10' E, latitude 55°42' N), 4.8 to 17.5 g DW m^{-2} by Kautsky (1987). Data on peak biomass in the tropics are scarce, but generally in the same order of magnitude as those in a temperate climate, i.e., 370-445 g DW m^{-2} (approximate longitude 78°28' E, latitude 17°27' N (Sinha 1970; Sahai and Sinha 1973). The highest published value on maximum biomass ($\leq$ 1,952 g DW m^{-2}) has been used to form the upper limit of plant biomass in the model.

Sago pondweed exhibits clonal growth consisting of the production through the season of potentially interdependent, nonperennating plants, followed by the development of tubers, which become independent ramets upon disintegration of the parent plants in early fall. Since currently no evidence of interdependency of sago pondweed has been published, all intact plants and tubers produced in one season from an initial tuber are viewed as individual plants in the model.

Typical plant density is 30 plants m^{-2}. It has been computed by dividing the maximum standing crop of an established monotypic sago pondweed vegetation at an anchorage depth of 2.5 m with a value of 82.27 g DW m^{-2} (Appendix C) by the highest average weight of an individual plant with neighbor plants (2.76 g DW $plant^{-1}$) in shallow waters studied in The Netherlands and the Camargue, France (Van Wijk 1989). Other literature reviewed did not provide sufficiently detailed information to enable calculations of plant density. Most of these studies dealt largely with weights of shoots composed by one stem with or without branches (e.g., Sher-Kaul et al. 1995), while whole plants are usually composed of several stems. Typical plant density indicates in the current case that it is possible that at some point in time different plant densities may occur, but that a typical established monotypic sago pondweed vegetation optimizes at 30 plants m^{-2}. Lower densities may occur in the establishment phase, where some plants may not yet have neighbors and become relatively large, while higher plant densities may occur early in the season when > 30 tubers m^{-2} have sprouted but the plantlets are subsequently thinned to 30 plants m^{-2} by self-shading of the vegetation.

In POTAM, plant density has been set to 30 plants m^{-2}. This implies that plant density at the beginning of the growth season is in principle 30 m^{-2}. Thus, the number of sprouting tubers in the tuber bank is 30 m^{-2}, while the remaining tubers continue to senesce. However, at tuber bank densities lower than 30 m^{-2}, the number of sprouting tubers is recalculated and set equal to the actual tuber bank density. If wintering plants are present, plant biomass is redistributed over 30 plants m^{-2}.

Wintering and Sprouting of Tuber Bank

Tubers are the main storage organs for carbohydrates in wintering sago pondweed in a temperate climate. In tubers, concentrations of total carbohydrate reserves may reach 68-74 percent dry weight (Appendix C; Hodgson 1966), starch may reach 53 percent, and soluble sugars 17 percent dry weight (Appendix C). Tuber biomass is usually 0 in early summer and reaches a maximum in autumn. Because in most papers either plant biomass and tuber numbers without tuber biomass, or tuber numbers and biomass without plants are presented, it is difficult to present an accurate estimate of the tuber biomass range. Another complicating factor is that individual tuber weight varies substantially.

Tuber densities in sago pondweed tuber banks may vary over a large range, from 0 in early summer to a maximum of 3,975 m^{-2} in autumn (Van Wijk 1989). The large range found is probably due to (a) the patchy spatial distribution of the community over the water body, (b) limited number of replicate samples taken

(Spencer et al. 1994), and (c) between site variation in anchorage depth of the vegetation.

The following densities have been published: (a) 45-115 m^{-2} on a wave-exposed shallow site within the fresh-brackish Baltic Sea, Sweden (Kautsky 1987); (b) 270-385 m^{-2} in the shallow, fresh Lake Veluwe, The Netherlands (Van Dijk et al. 1992); (c) 1,330 and 3,975 m^{-2} in the oligohaline, sheltered ditch Salin De Badon and shallow pool Les Garcines, respectively, both in the Camargue, France (Van Wijk 1988); (d) 10 and 18 tuber size classes with average tuber weights of 0.061 ± 0.006 g fresh weight (range 0.02 to 0.3 g) and of 0.017 ± 0.003 g fresh weight (range 0.02 to 0.46 g) in the fresh Lake Veluwe and a brackish Texel ditch, respectively, both in The Netherlands (Vermaat and Hootsmans 1994a).

Published tuber weights (g dry weight tuber^{-1}) are (a) 0.005 to 0.155 (0.013 g on average; growth chamber study in California (Spencer and Anderson 1987)); (b) 0.017 (derived from 0.056 g fresh weight, and a dry:fresh weight ratio of 0.299 ± 0.034; harvested from freshwater irrigation canals in central California (Spencer 1987)); (c) 0.083 (Appendix C).

Tubers may lie dormant if not disturbed, and it is, therefore, to be expected that maintenance processes proceed at a very low level of activity. Tuber weight may decrease by tuber death and by the sprouting of tubers, which transform into plants. Tuber density may decrease by grazing by waterfowl and other animals. Both tuber weight and density may increase by the formation of new tubers (this chapter, section, "Induction and Formation of New Tubers").

Sprouting potential is substantial even without stratification, but it is increased by cold stratification during 4-10 weeks (Van Wijk 1989). Sprouting potential of the tubers is usually high in a temperate climate, being ≤ 80 percent. Sprouting frequency in an established community is probably not important, unless it is very low, as long as the typical plant density of 30 plants m^{-2} is somehow reached, since plant density tends to play a lesser role in biomass production compared to space availability. Actual sprouting frequency under natural conditions is unknown. Sprouting frequency decreases with tuber burial depth: (a) small tubers in the size range of 0.003 to 0.012 g DW proved less likely to emerge when planted at 5 and 10 cm than at 2.5-cm depth; (b) only 30 percent of large tubers weighing 0.017 g DW sprouted at 20-cm depth (Spencer 1987).

Whether or not sprouting is affected by day length and/or illumination is not known, but growth of sprouts from tubers was not (Spencer and Anderson 1987; Van Wijk 1989). Abundant sprouting was observed between 5.5 and 10 °C in the Western Canal near Zandvoort, The Netherlands (Appendix C), and 25 °C (Spencer and Anderson 1987, California; Van Wijk 1989, France); but sprouting was lower at 25° than at 20 °C (Van Wijk 1989). Sprouting usually takes place early in the season. The earliest date mentioned is the beginning of April, when the first shoots were observed in the Western Canal, The Netherlands, in 1987 (Appendix C).

Death rates of tubers have not been published. The value for the relative death rate of tubers, *RDTU*, was found by applying the same differential equation as commonly used for simple exponential growth to describe continuous exponential decrease in tuber number, with a negative specific decrease rate (Thornley and Johnson 1990b; Hunt 1982). An *RDTU* of 0.026 d^{-1} (on number basis) was found for the sago pondweed population in a shallow ditch in Yerseke, The Netherlands, by converting tuber standing crop values (Figure 6 in Van Wijk 1988) into tuber numbers using Table 2 of Van Wijk (1988). Somewhat lower *RDTU* values were found for other populations studied by Van Wijk. The latter *RDTU* value is far lower than that of 0.36 d^{-1} for hydrilla tubers estimated from simulations alone because virtually no seasonal changes in hydrilla tuber data had been published at that time (Best and Boyd 1996). Both plant species are expected to lose tubers through grazing by waterfowl, which may affect the amount of tubers sampled (and published). However, the relatively lower loss in sago pondweed may be explained by the relatively low tuber bank density of this plant (5-10 times higher in hydrilla), which may discourage foraging by waterfowl because it may require a relatively long search time as found for *Vallisneria americana* (Lovvorn 1989; Lovvorn and Gillingham 1996).

Higher temperatures expedite turnover rates of plant tissues and increase maintenance costs. A temperature increase of 10 °C usually increases maintenance respiration by a factor of about 2 up to temperatures that usually kill plants (45 to 60 °C; $Q_{10} = 2$ at a reference temperature of 20 °C (Penning de Vries et al. 1989a)). The value of 2 for Q_{10} appears to be a reasonable average, but lower and higher values have been reported also (Amthor 1984).

In POTAM, initial tuber biomass has been set at 19.92 g dry weight m^{-2}. The latter value was calculated by multiplication of the measured tuber number per plant (8 $plant^{-1}$) and mean tuber weight (0.083 g DW $tuber^{-1}$) at a 1.0-m anchorage depth in the Western Canal near Zandvoort (Appendix C), by the commonly found plant density (30 m^{-2}), resulting in 240 tubers m^{-2}.

Sprouting is a function of development phase through the 3 °C day-degree sum; it occurs between DVS 0.211 and the flowering period of the plant population. Sprouting frequency has been set equal to the number of plants per surface area, i.e., at 30 sprouts m^{-2}.

The relative tuber death rate is set at 0.026 d^{-1}. It is presumed to be influenced by temperature through a relative effective temperature function, *TEFF*. This function describes processes relative to a reference temperature of 20 °C at which the function has the value of 1, to increase with a Q_{10} of 2 at temperatures > 20 °C, to increase between 0 and 5 °C from 0.0001 to 0.5, and to decrease with a Q_{10} of 2 at temperatures < 20 °C. A similar approach to account for temperature effects on maintenance respiration has been followed by Thornley and Johnson (1990a).

Initial Growth of Sprouts

Tubers sprout and plantlets initially elongate, depleting the tuber carbohydrate reserves (starch up to 53 percent DW (Appendix C)). Sprouting can occur only in tubers weighing at least 0.001 g DW tuber^{-1} (Spencer 1987).

Whether or not these plantlets survive at the plant height they can maximally reach by merely depleting their carbohydrate reserves depends on the size and the carbohydrate efflux due to growth respiration of the tuber, and the carbohydrate influx in the plants because of photosynthesis.

The elongation potential of sprouts emerging from tubers is limited, i.e., 0.00714 m for tubers ranging in weight from 0.0054 to 0.155 g DW tuber^{-1} (Spencer 1987; Spencer and Anderson 1987). Thus, plants can rise one layer 0.1 m deep in the water column only when they can fill that layer with a minimum of 0.0076 or maximum of 0.2170 g plant DW.

Respiration of tubers is low when tubers are in a dormant state. A rate of 0.00312 g CO_2 tuber^{-1} day^{-1} at 10 °C was derived from measurements in 0.083 g DW dormant tubers (Appendix C). This is based on the following: (a) dormant tuber respiration rate is 0.003623 ± 0.0003 g CO_2 g DW^{-1} h^{-1} at 20 °C; (b) temperature influences respiration as described in the section "Wintering and Sprouting of Tuber Bank." This means that the latter tuber can survive for 27 days after sprouting if light for photosynthesis is lacking (0.00312 g CO_2 tuber^{-1} day^{-1} × 27 days = 0.083 g tuber). Consequently, sprouting tubers of this size die after a survival period of 27 days without net photosynthesis taking place. Larger tubers have longer and smaller tubers shorter survival periods.

In the model, tuber bank weight is calculated from initial tuber number and individual tuber weight read from the input file.

Tubers sprout, provided conditions allowing sprouting are met: (a) proper degree-day sum and (b) sufficient tuber bank weight.

Remobilization of tuber carbohydrates occurs by sprouting. Remobilization is the conversion of part of the carbohydrate reserves into sprout material via a relative tuber-to-plant conversion rate (*ROC*). For *ROC* of sago pondweed, the same value as for hydrilla tubers was used (0.0576 g CH_2O g tuber DW^{-1} d^{-1} (Best and Boyd 1996)). These carbohydrates are allocated to the plant organs following a fixed biomass partitioning pattern (see section "Light, Photosynthesis, Maintenance, Growth, and Assimilate Partitioning in Sago Pondweed Plants"). Elongation occurs by filling each successive water layer from hydrosoil to the water surface with the minimum shoot biomass required (0.0076 g plant DW plant^{-1}, termed *CRIFAC*). Remobilization and subsequent growth continue until the carbohydrates of the sprouting tubers are depleted.

Sprouting tubers die if the resulting plant biomass has a negative net assimilation rate over a user-defined number of days (*SURPER*; 27 days is nominal), and the program stops with a warning *KCOUNT*.

After the death of one tuber class, one or more other tuber classes can sprout, provided tubers are available and the day-degree sum (Table 1) is lower than required for flowering. The program can resume running for the same year after the user presses **ENTER** provided the proper conditions are met.

A relational diagram illustrating the wintering and sprouting tubers of sago pondweed is shown in Figure 2.

The following equations describe wintering and sprouting of the tuber bank:

$TWGTUB = NPL \times INTUB$

$NDTUB = NDTUB - (NTUBD - NTUBPD)$

$NTUBD = RDTU \times NDTUB \times TEFF$

$IF\ (DVS.\ GE.\ 0.291.\ AND.\ DVS\ .LT.\ 1.)\ THEN$

$IF\ (TWGTUB\ .LE.\ (0.01 \times NPL \times INTUB))\ NGTUB = 0.0$

$NGTUB = NPL$

$TWGTUB = INTGRL\ (TWGTUB,\ -REMOB,\ DELT)$

$REMOB = TWGTUB \times ROC \times TEFF$

where

$TWGTUB$ = total dry weight of sprouting tubers (g DW m^{-2})
NPL = plant density (plants m^{-2})
$INTUB$ = initial dry weight of a tuber (g DW tuber^{-1})
$NDTUB$ = dormant tuber number (dormant tubers m^{-2})
$NTUBD$ = dead tuber number (dead tubers m^{-2})
$NTUBPD$ = dead tuber number of the previous day (dead tubers m^{-2})
$RDTU$ = relative death rate of tubers (on number basis; d^{-1})
$TEFF$ = factor to account for temperature effect on maintenance respiration, remobilization, and maximum relative tuber growth rate (-)
DVS = development phase of the plant (-)
$NGTUB$ = sprouting tuber number (sprouting tubers m^{-2})
$REMOB$ = remobilization rate of carbohydrates (g DW m^{-2} d^{-1})
ROC = relative conversion rate of tuber into plant material (g CH$_2$O g DW^{-1} d^{-1})
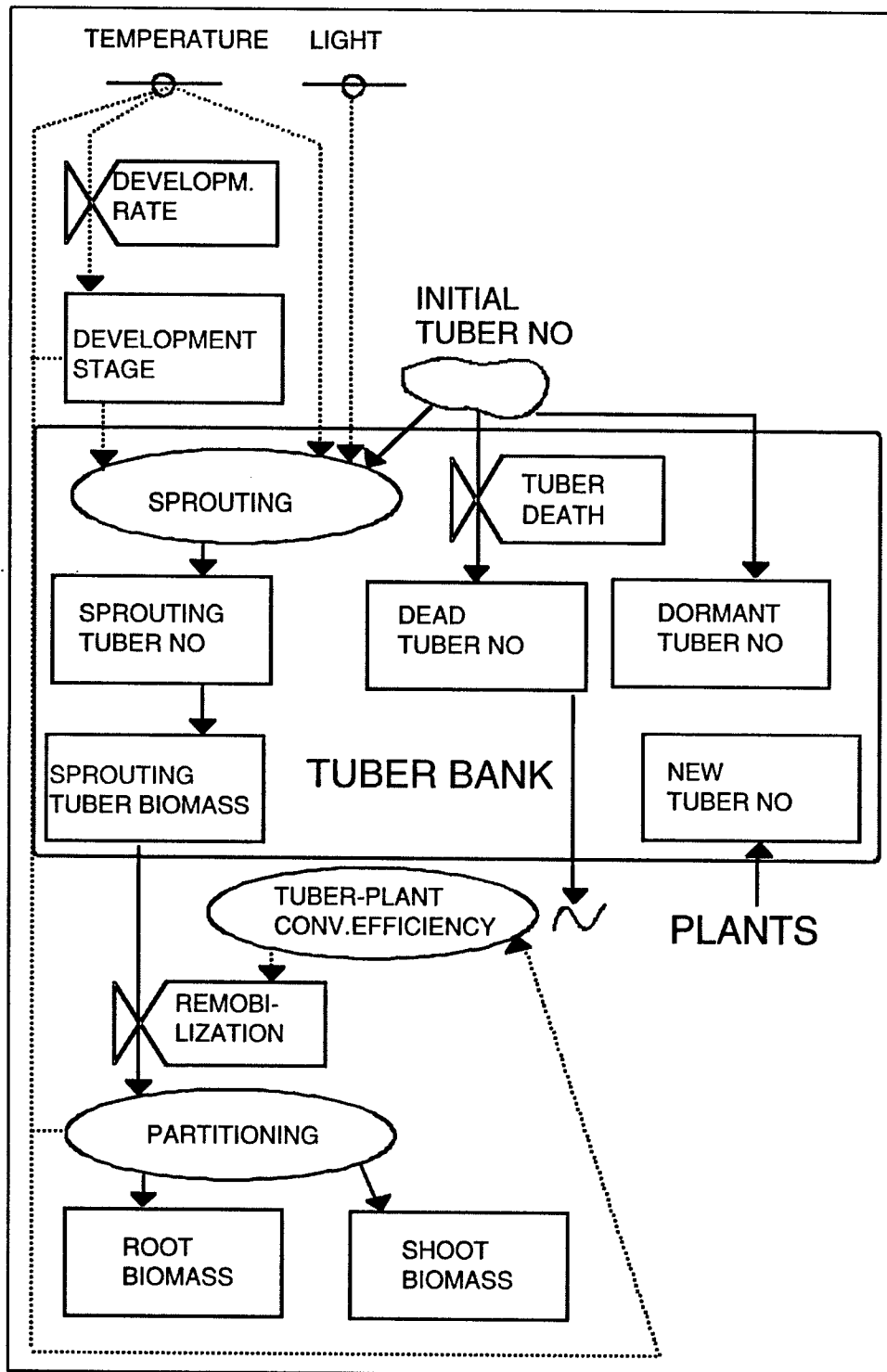
Figure 2.   Relational diagram illustrating the wintering and sprouting of tubers in sago pondweed

Light, Photosynthesis, Maintenance, Growth, and Assimilate Partitioning in Sago Pondweed Plants

Light

Light availability is an important factor controlling the distribution and abundance of submersed macrophytes. In aquatic systems light can be attenuated rapidly by water and its suspended solids, and by macrophytes themselves. A relatively small part of the irradiance can be reflected by the water surface.

In the model, the measured daily total irradiance (wavelength 300-3000 nm) is used as input. Only half of the irradiance reaching the water surface is considered to be photosynthetically active and is, therefore, used to calculate CO_2 assimilation. Six percent of the irradiance is reflected by the water surface (Golterman 1975).

The subsurface irradiance is attenuated by dissolved substances and particles within the water column resulting in a site- and season-specific extinction coefficient. Moreover, the vertical profiles of the radiation within the plant community layers are characterized. The absorbed irradiance for each horizontal community layer is derived from these profiles. The community-specific extinction coefficient, K, is assumed to be constant throughout the year and given a value of 0.095 m^2 g DW^{-1} measured in the canopy of a sago pondweed community in the Western Canal near Zandvoort, The Netherlands (Appendix C). Other lower community-specific extinction coefficients of 0.0183 and 0.020 m^2 g DW^{-1} have been found by Sher-Kaul et al. (1995) and Westlake (1964) (used in a different sago pondweed growth model by Hootsmans 1991).

The incoming irradiance is attenuated by the shoots, part of which is absorbed by the photosynthetic plant organs, i.e., the leaves.

$$IRZ_{i+1} = IRZ_i \times e^{(-TL \times L - K \times SC_i)}$$

$$IABS_i = \frac{(IRZ_i - IRZ_{i+1}) \times SC_i \times K}{(K \times SC_i + TL \times L)} \quad (3)$$

$$IABSL_i = IABS_i \times FL$$

where
IRZ_i = photosynthetic active part of total irradiance on top of depth layer i (J m^{-2} s^{-1})
TL = thickness depth layer (0.10 m)
L = light extinction coefficient of water (m^{-1})
K = plant-specific extinction coefficient (m^2 g DW^{-1})
SC_i = shoot dry matter in depth layer i (g DW m^{-2})
$IABS_i$ = total irradiance absorbed in depth layer i (J m^{-2} s^{-1})
$IABSL_i$ = total irradiance absorbed by plant shoots in depth layer i (J m^{-2} s^{-1})
FL = leaf dry matter allocation to each layer of the vegetation (relative; -)

Photosynthesis

In the model, the instantaneous rates of gross assimilation are calculated from the absorbed light energy and the photosynthesis light response of individual shoots, here used synonymously with leaves.

The photosynthesis light response of leaves is described by the exponential function

$$FGL = SC_i \times AMAX \times \left(1 - \exp\left[\frac{-EE \times IABS_i \times 3600}{AMAX \times SC_i}\right]\right) \tag{4}$$

where

FGL = instantaneous gross assimilation rate per depth layer (g CO_2 m^{-1} h^{-1})

$AMAX$ = actual CO_2 assimilation rate at light saturation for individual shoots (g CO_2 g DW^{-1} h^{-1})

EE = initial light-use efficiency for shoots (g CO_2 J^{-1} absorbed)

For photosynthetic activity at light saturation (AMX) the value of 0.019 g CO_2 g DW^{-1} h^{-1} was used. This value was calculated by converting the maximum net oxygen production of sago pondweed apices in May of 13.5 mg O_2 g DW^{-1} h^{-1} into mg CO_2 g DW^{-1} h^{-1}. The plant population studied grew in the shallow, fresh River Susa, Denmark (Van der Bijl et al. 1989). In Van der Bijl's study, photosynthetic activity of apices always greatly exceeded that of intermediate and basal plant parts, and was usually in the order of 0.012 g CO_2 g DW^{-1} h^{-1} during summer. A lower value for AMX of 0.0099 g CO_2 g DW^{-1} h^{-1} was found by Vermaat and Hootsmans (1994b; Chapter 6) for sago pondweed from a shallow freshwater lake incubated in the laboratory. Using the latter value for runs into their SAGA model indicated that a 20 percent increased AMX, i.e., of 0.012 g CO_2 g DW^{-1} h^{-1}, was required to generate realistic plant biomass results. An even lower value for AMX of 0.0055 g CO_2 g DW^{-1} h^{-1} was found by Madsen and Adams (1988) for sago pondweed from a freshwater river incubated in the laboratory.

Light- and carbon-saturated photosynthetic rates of sago pondweed can be far higher (0.039 g CO_2 g DW^{-1} h^{-1}) (Appendix C), suggesting that photosynthetic activity in waters with low dissolved inorganic carbon concentrations (< 3.5 mmol L^{-1}) or high pH (> 8) can be carbon limited.

Gross assimilation rate at light saturation shows a distinct seasonal pattern and tends to decrease with aging (Appendix C; Van der Bijl et al. 1989). Although a function describing this relationship ($AMDVST$) has been included in the model, it is not active in the nominal version (it has the value of 1) since running the model showed that it was not quantitatively important.

Daily changes in pH and oxygen concentrations may affect AMX. A reduction factor, $REDAM$, can be used to take these effects into account by reducing the AMX by a factor between 0 and 1 for the whole day. $REDAM$ currently has the value of 1, because pH in the sago pondweed communities in the Western Canal

near Zandvoort oscillated around 8.4 (Appendix C), where actual and potential photosynthetic activities at light saturation are similar. Sensitivity of sago pondweed to changes in oxygen concentration is unknown, and is not accounted for in the model.

Changes in temperature affect *AMX*. A fitted, relative function, *AMTMPT*, describes the effect of daytime temperature on *AMX*, which is based on the measured photosynthetic response of sago pondweed to temperature and has its optimum at 30 °C (Appendix C; Madsen and Adams 1988).

For photosynthetic light-use efficiency (*EE*), a value of 11×10^{-6} g CO_2 J^{-1}, typical for C_3 plants, was used (Penning de Vries and Van Laar 1982a). Substituting the appropriate value for the absorbed photosynthetically active radiation yields the assimilation rate for each specific shoot layer.

The instantaneous rate of gross assimilation over the height of the plant community is calculated by relating the assimilation rate per layer to the community-specific biomass distribution and by subsequent integration of all community layers.

The daily gross assimilation rate is calculated using the Gaussian integration method. This method specifies the discrete points at which the value of the function to be integrated has to be calculated, and the weighting factors that must be applied to these values to attain minimum deviation from the analytical solution. A three-point method performs very well for calculating daily total assimilation (Goudriaan 1986; Spitters 1986).

Maintenance, growth, and assimilate partitioning

Maintenance. Some of the carbohydrates formed are respired to provide energy for maintaining the existing plant components. The maintenance costs increase with metabolic activity, probably because of higher enzyme turnover and higher transport costs (Penning de Vries 1975).

The maintenance cost can be estimated from the chemical composition of the plant. Typical maintenance coefficients for various plant organs have been derived, based on numerous chemical determinations in agricultural crops. They typically range from 0.010 to 0.016 g CH_2O g ash-free dry weight $(AFDW)^{-1}$ d^{-1} (Penning de Vries and Van Laar 1982b).

In POTAM, the maintenance coefficients already mentioned are used to calculate the maintenance requirement of the plants. Maintenance respiration has been related to temperature by the same relative effective temperature function as used for the remobilization and relative tuber growth and death rates. Maintenance costs for the tubers have been discussed earlier in the section "Wintering and Sprouting of Tuber Bank."

The following equations describe maintenance costs for sago pondweed plants:

$$MAINTS = 0.016 \times TWLG + 0.010 \times TWSG + 0.015 \times TWRG$$
$$MAINT = MAINTS \times TEFF \qquad (5)$$

where

$MAINTS$ = maintenance respiration rate of the vegetation at reference temperature (g CH_2O m^{-2} d^{-1})

$TWLG$ = total dry weight of live leaves (g DW m^{-2})

$TWSG$ = total dry weight of live stems (g DW m^{-2})

$TWRG$ = total dry weight of live roots (g DW m^{-2})

$MAINT$ = maintenance respiration of the vegetation (g CH_2O m^{-2} d^{-1})

$TEFF$ = factor accounting for effect of temperature on maintenance respiration (-)

Growth. Assimilates in excess of maintenance costs are available for conversion into structural plant material. In this conversion process of the glucose molecule, CO_2 and H_2O are released. The assimilates required to produce one unit weight of any particular plant organ can be calculated from its chemical composition and the assimilate requirements of the various chemical components. Typical values are 1.46 g CH_2O g DW^{-1} for leaves, 1.51 for stems, and 1.44 for roots (Penning de Vries and Van Laar, 1982b; Penning de Vries et al. 1989a), confirmed by Griffin (1994). At higher temperatures the conversion processes are accelerated, but the pathways are identical. The recently determined construction costs for several submersed plant species using a different method (Williams et al. 1987) are generally lower, ranging from 0.99 to 1.11 (Spencer et al. 1997). However, some of the latter plants are relatively poor in nitrogen and transport costs have not been included, both factors which may have contributed to the lower cost found.

In POTAM the construction costs typical for agricultural plants have been used, since construction costs calculated for sago pondweed leaves with an average chemical composition were similar to those in agricultural plants, i.e., 1.465 CH_2O g DW^{-1} (for calculation costs for leaves, see Appendix C), and stems and roots were presumed to be similar also.

The following equation describes growth:

$$GTW = \frac{\left[(REMOB \times CVT) + GPHOT - TRANS - MAINT \right]}{ASRQ} \qquad (6)$$

where

GTW = dry matter growth rate of the vegetation (plants excluding tubers) (g DW m^{-2} d^{-1})

$REMOB$ = remobilization rate of carbohydrates (g CH_2O m^{-2} d^{-1})

CVT = conversion factor of translocated dry matter into CH_2O (-)

$GPHOT$ = daily total gross assimilation rate of the vegetation (g CH_2O m^{-2} d^{-1})

$TRANS$ = translocation rate of carbohydrates (g CH_2O m^{-2} d^{-1})

$MAINT$ = maintenance respiration rate of the vegetation (g CH_2O m^{-2} d^{-1})

$ASRQ$ = assimilate requirement for plant dry matter production
$\quad$ (g CH$_2$O g DW^{-1})

Assimilate partitioning. Assimilate partitioning is the process by which assimilates available for growth are partitioned over leaves, stems, roots, and/or storage organs. It depends on physiological age. Assimilate partitioning pattern in sago pondweed is not known. However, the biomass resulting from this process was partitioned for 80.0 percent over leaves, 12.5 percent over stems, and 7.5 percent over roots as documented in two well-developed sago pondweed communities in summer in The Netherlands (Appendix C; Sher-Kaul et al. 1995). These values are close to those published by Spencer and Anderson (1987), i.e., 90 percent over shoots and 10 percent over roots, with photoperiod having no effects.

Sago pondweed exhibits a typical umbrella-shaped depth distribution of shoot biomass from the top of the vegetation downwards. In a full-grown sago pondweed community in the Western Canal, The Netherlands, 78 percent of shoot biomass was found within 0.5 m of the sediment/water interface (Yeo 1965; Howard-Williams 1981; Appendix C).

In POTAM, assimilate partitioning is used synonymously with biomass partitioning, with the latter following the same distribution pattern as measured in full-grown plants, starting from the time when the shoot tips have reached the water surface.

Shoot biomass is allocated over the vertical axis via a dry matter partitioning coefficient function (DMPC) following the typical umbrella type shape. Allocation proceeds as follows. First plant biomass is allocated for 78.4 percent to the five depth layers starting from the water surface downwards, with a depth distribution of successively 4.3, 4.3, 23.1, 25.4, and 21.3 percent. Allocation to the layers below this 0.5 m is equal up to a total plant biomass share of 13 percent. When the amount of biomass allocated to a water/plant layer is lower than the critical biomass required to support plant biomass above that layer, the total number of plant layers is reduced with one and the biomass allocation procedure is redone. When five or fewer water layers are present, first the upper water layers are filled according to allocation pattern, and subsequently the remaining plant biomass is added and distributed equally over the found water layers. Roots always contribute 8.6 percent to total plant biomass. Vertical biomass distribution pattern is recalculated and redistributed by POTAM when an anchorage depth other than nominal (1.3 m) is chosen.

The following equation describes biomass partitioning over plant organs:

$$GLV = FLV \times GTW$$
$$GRT = FRT \times GTW$$
$$GST = FST \times GTW$$

$$(7)$$

where FLV, FRT, and FST are fractions of total dry matter increase allocated to leaves, roots, and stems, respectively (relative); GLV, GRT, and GST are dry

matter growth rates of leaves, roots, and stems, respectively (g DW m^{-2} d^{-1}); and *GTW* is dry matter growth rate of the vegetation (plants excluding tubers) (g DW m^{-2} d^{-1})

A relational diagram illustrating photosynthesis, respiration, and biomass formation of sago pondweed is shown in Figure 3.
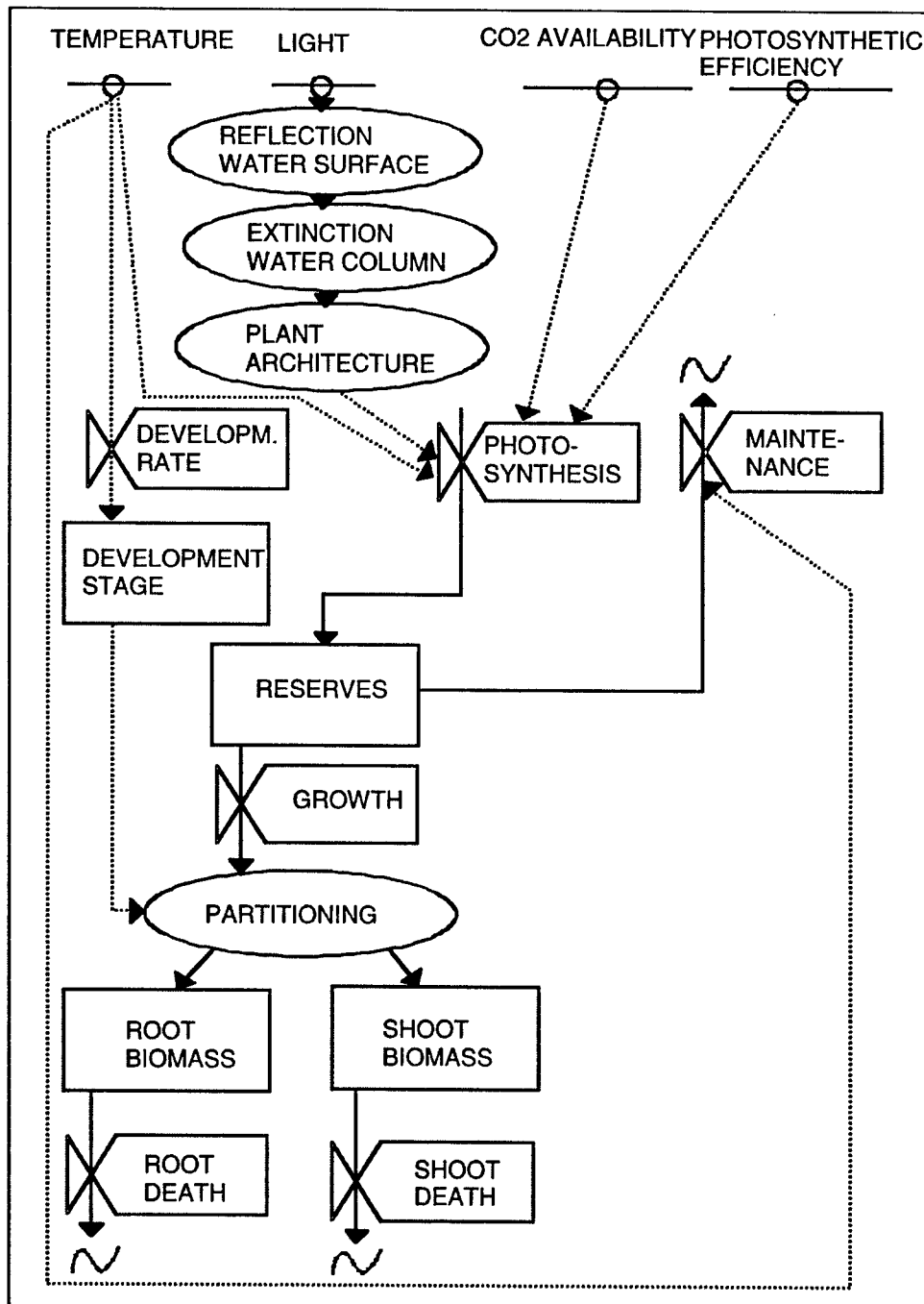
Figure 3.   Relational diagram illustrating photosynthesis, respiration, and biomass formation in sago pondweed

Induction and Formation of New Tubers

Tubers are formed just after flowering under relatively short day conditions (between 10 and 16 hr light per day) and within a temperature range between 5.5 and 25 °C. This was concluded largely from two studies. Experiments by Spencer and Anderson (1987) in California indicated that sago pondweed plants grown at photoperiods varying between 10 and 16 hr light per day for periods up to 56 days exhibited enhanced tuber production at a photoperiod between 10 and 12 hr. Moreover, vegetative propagules appeared to be produced instead of shoot tissue under short-day conditions. A field study on Lake Veluwe, The Netherlands, revealed a sharp increase in tuber production after 15 July (air temperature 12 °C, day length 16 hr) with maximum tuber number reached at 23 August (air temperature 21 °C, day length 13 hr (Table 3 in Van Wijk 1988). It is possible that tuber induction in sago pondweed is triggered by phytochrome and is associated with increased abscisic acid levels, as in hydrilla (Van et al. 1978; Klaine and Ward 1984), *Ceratophyllum demersum* (Best 1982), and the terrestrial potato (Kooman 1995).

Tubers can be formed only by a plant (not by an already existing tuber). Environmental conditions favoring tuber formation occur in a temperate climate in spring and late summer. Since in this climate sago pondweed winters by tubers without plants, tubers can be formed only in late summer. However, in other warmer climates where sago pondweed may winter by plants and tubers, tuber formation may follow a different timing.

Tubers grow from assimilates translocated downward from the shoots. Translocation has not been measured in submersed plants. However, estimates based on data pertaining to other plants are 19 percent of net production in seagrasses (Wetzel and Neckles 1996), 35 percent in Eurasian watermilfoil (Best and Boyd 1996), and approximately 40 percent in hydrilla (Best and Boyd 1996). In terrestrial tuber-producing plants translocation was 29 percent of net production in cassava (Gijzen 1985) and 35 percent in certain potato varieties (Kooman 1995). The translocated material consisted largely of carbohydrates, and was considered as equivalent to starch (Gijzen 1985).

Individual tuber weight and tuber number concurrently formed by each plant depend on the photoperiod at which the plant grows. Individual tuber weight increased linearly with tuber number concurrently formed per plant at a photoperiod of ≤ 12 hr light per day from 1 tuber with a weight of 0.016 g DW tuber^{-1} to 12 tubers with a mean weight of 0.155 g DW tuber^{-1} for plants grown for 56 days (Figure 4; Spencer and Anderson 1987). The plant material for this study originated from Omro, WI (longitude 44°02' W, latitude 48°44' N) while the study was performed in a growth chamber in Davis, CA (longitude 121°48' W, latitude 38°33' N). This response to a short-day photoperiod is similar to that exhibited by *Hydrilla verticillata* L. (Van et al. 1978; Sutton et al. 1980; Klaine and Ward 1984; Spencer and Anderson 1986), *Utricularia vulgaris* L. (Winston and Gorham 1979), *Myriophyllum verticillatum* L. (Weber and Nooden 1974), and *Hydrocharis morsus-ranae* (Terras 1900). Tuber production was far (> 75 percent) lower in plants grown at 14- or 16-hr photoperiods than in plants cultivated at a 10-hr photoperiod. The light level at which the plant grows is also

important, since tuber weight increased about ten times with a doubling of the growth period (Spencer and Anderson 1987). This led to the conclusion that sago pondweed may follow an optimization strategy aimed at forming the largest possible tubers at the light level experienced, possibly because large tubers have a greater survival value than smaller ones. Based on the assumption that the plant follows this optimization strategy, an established plant population growing at a given light level will aim at forming only one tuber weight class, i.e., with an individual tuber weight that allows new plants to survive at that site. Consequently, the differences in tuber weights found in tuber banks may be explained by difference in age between tuber classes, with the oldest class having a lower weight because the tubers have lost weight by senescence, and the youngest class having a lower weight because the tubers were not completely finished before the plants were fully senesced.
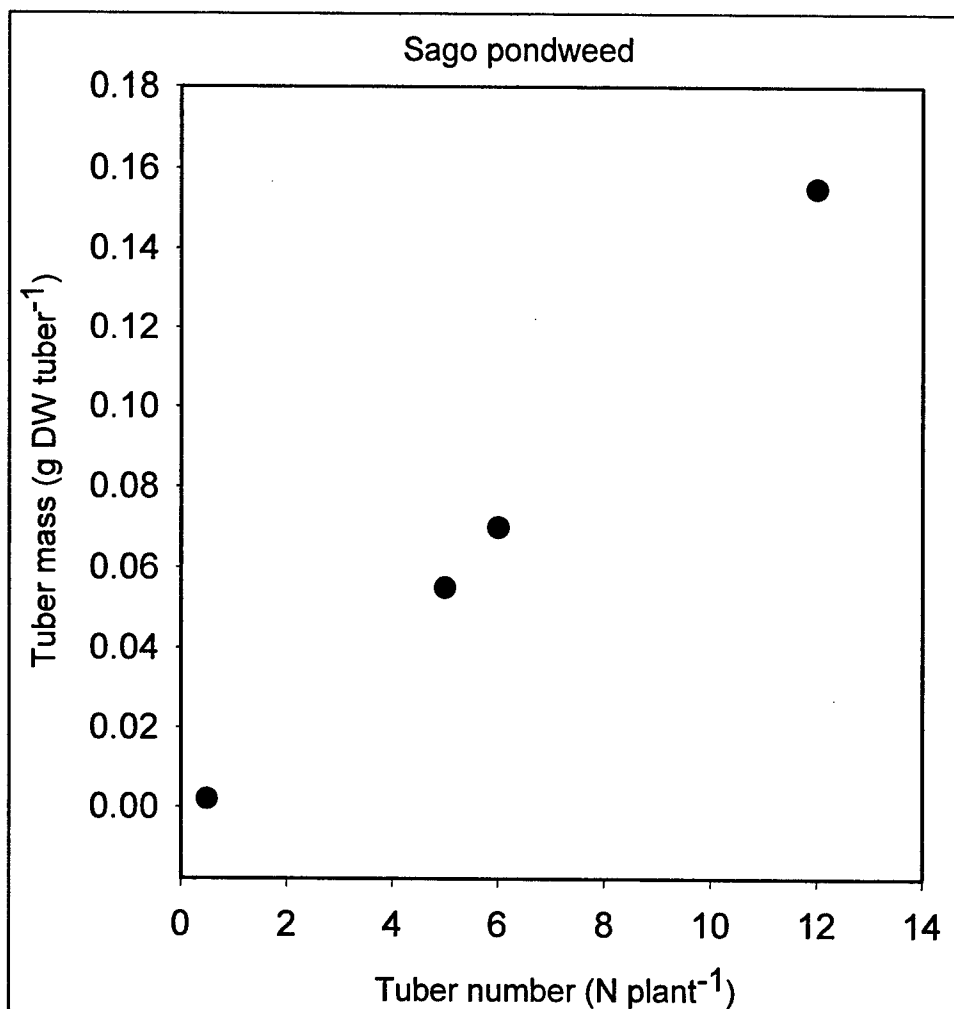
Figure 4. The relationship between tuber number concurrently initiated per plant and tuber size for sago pondweed (data from Spencer and Anderson 1987)

In the model, induction of tuber formation occurs at DVS > 1.0, daylength < 16 hr, and a temperature range of 5 to 25 °C. Once initiated, a tuber class grows from translocated material until a preselected individual tuber weight is reached.

Nominal values are 8 tubers with an 0.083-g-DW individual tuber weight making up a 19.92-g-DW critical tuber weight class (*TWCTUB*; 8 × 0.083 × 30). Transport of glucose costs dry matter, i.e., 36/38, whereas conversion of starch into glucose increases the dry matter with a factor 10/9. Thus, the total transport "cost" of downward translocation is a factor *CVT* = 1.05 (10/9 × 36/38). The intensity of translocation is governed by the maximum relative growth rate of the tubers, *RTRL*, that consumes 19 percent of net production by the senescing plants, multiplied by *CVT*. This relative growth rate was found by applying the same differential equation as commonly used for simple exponential growth (Thornley and Johnson 1990b; Hunt 1982) to tuber data collected in the field (Table 1 in Van Wijk et al. 1988). Thus a maximum relative growth rate of tubers of 0.19 d^{-1} at a reference temperature of 20 °C was computed. Temperature influences on the relative growth rate of tubers are described in the section "Wintering and Sprouting of Tuber Bank." Once finished, a tuber class is added to the dormant tuber bank, and the plant starts forming a new tuber class. Tuber initiation continues as long as environmental conditions permit, and tubers are formed as long as the plants can provide assimilates to fill them.

The following equations describe induction and formation of new tubers.

IF (REMOB . EQ. 0.0) THEN
IF (DVS. GT. 1.0. AND. DAYL. LT. 14.7)THEN
IF (DDTMP .GT. 5.0 .AND. DDTMP .LT. 25.0)THEN
IF (TGW .GT .0.1) THEN
TRANS = AMAX1 [0., (RTRL * 1./CVT) * (GPHOT – MAINT)]
NNTUB = NPL * NINTUB
TWNTUB = INTGRL (TWNTUB, TRANS, DELT)
IF (TWNTUB .GE. TWCTUB) THEN
NDTUB = NDTUB + (NPL * NINTUB)

where
    DAYL = day length (hr)
  DDTMP = daily average daytime temperature (°C)
     TGW = total live plant dry weight, excluding tubers (g DW m^{-2})
  TRANS = translocation rate (g CH$_2$O m^{-2} d^{-1})
   RTRL = relative tuber growth rate at ambient temperature (g DW tuber^{-1} d^{-1})
     CVT = conversion/transport factor (relative; -)
 GPHOT = daily total gross assimilation rate of the community (g CH$_2$O m^{-2} d^{-1})
  MAINT = maintenance respiration of the vegetation (g CH$_2$O m^{-2} d^{-1})
  NNTUB = new tuber number (new tubers m^{-2})
 NINTUB = tuber number concurrently initiated per plant (conc. initiated tubers plant^{-1})
TWNTUB = total dry weight of new tubers (g DW m^{-2})
TWCTUB = total critical dry weight of new tubers (g DW m^{-2})
  NDTUB = dormant tuber number (dormant tubers m^{-2})

Flowering and Senescence

The occurrence of flowering affects subsequent metabolic activity of the vegetation. The timing of flowering is, therefore, extremely important for the physiological activity and biomass formation, while the actual investment of dry matter in flowers and seeds proves to be only minor (Yeo 1965; Van Wijk 1989). After flowering, senescence sets in, resulting in loss of particulate plant material, while a considerable part of net production is translocated downward to the tubers with the remainder of net production being allocated following the typical pattern described in the subsection "Maintenance, Growth, and Assimilate Partitioning."

Senescence refers to the loss of capacity to carry out essential physiological processes and to the loss of biomass. The fundamental processes involve physiological aging and protein (enzyme) breakdown. These processes are difficult to quantify. It is known that hormones are important messengers in this context, but it is not known precisely how they act. High temperature usually accelerates senescence.

In POTAM, the timing and value of relative death rate (RDR) of the plants have been derived from field observations on plant biomass in the Western Canal near Zandvoort (1-m depth class) (Appendix C). A mechanistic approach to senescence has been chosen by setting the death rate at a certain fraction of plant biomass lost per day once the conditions for growth deteriorate. The timing of onset of senescence was found by running the model repeatedly with different development rates and base and reference temperatures until a good fit between simulated and measured values was accomplished. Thus, initiation of senescence for plants was set at DVS 2.001. The value for the relative death rate of the plants was found by applying the same differential equation as commonly used for simple exponential growth, to describe exponential decrease in biomass after flowering, with a negative specific decrease rate. Thus, an RDR of 0.047 d^{-1} was found for the period between peak biomass and several days before plant biomass had disappeared. The latter value was used in the model. It is presumed to increase with temperature between 20 and 50 °C through a relative temperature function. This function describes processes relative to a reference temperature of 20 °C at which the function has the value of 1, to increase with a Q_{10} of 2 at temperatures between 20 and 40 ° C, and to increase further to the value of 1 at 50 °C.

A relational diagram illustrating translocation and senescence is shown in Figure 5.
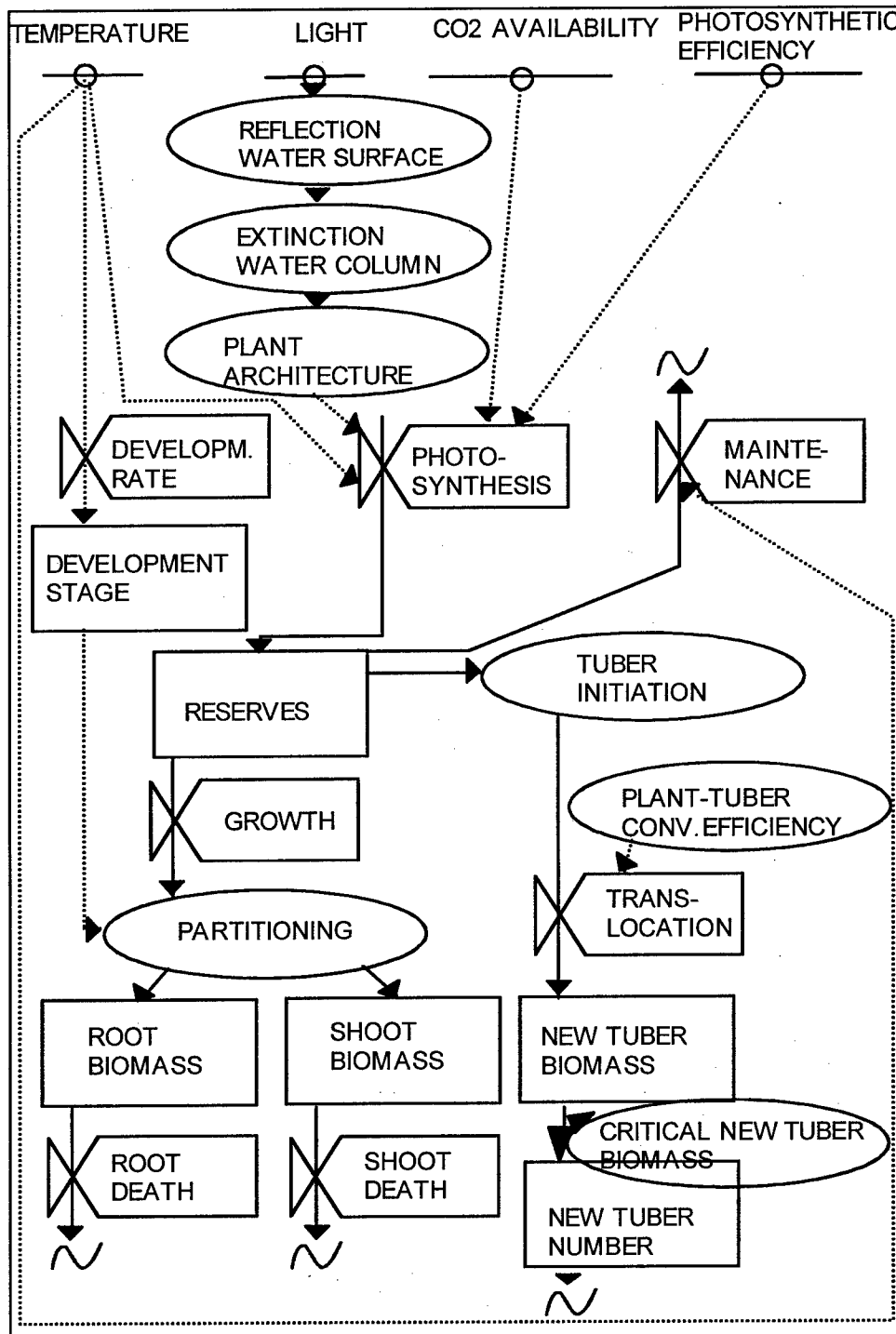
Figure 5. Relational diagram illustrating translocation and senescence following anthesis in sago pondweed

Choice of Parameter Values

A relatively simple simulation model like POTAM includes parameter values that can be defined with varying certainty. Most parameters have been

calculated/estimated from published literature (Table 2). Only development rate in relation to 3 °C day-degree sum and base temperature have been calibrated by running the model. The choice of parameter values has been detailed in the preceding sections of this chapter.

Table 2
Parameter Values Used in POTAM

Parameter	Abbreviation	Value	Reference
Morphology, Phenological Cycle, and Development			
First Julian day number	DAYEM	1	
Base temperature for juvenile plant growth	TBASE	3 °C	calibrated
Development rate as function of temperature	DVRVT*	0.015	calibrated
DVR prior to flowering (DVRVT), DVR subsequently (DVRRT)	DVRRT*	0.040	
Fraction of total dry matter increase allocated to leaves	FLVT	0.731	1,2
Fraction of total dry matter increase allocated to stems	FSTT	0.183	1,2
Fraction of total dry matter increase allocated to roots	FRTT	0.086	1
Maximum Biomass and Plant Density			
Maximum biomass		1,952 g DW m^{-2}	3
Plant density	NPL	30 m^{-2}	1,4
Wintering and Sprouting of Tuber Bank			
Initial tuber density	NT	240 m^{-2}	1
Initial dry weight per tuber	INTUB	0.083 g DW. tuber^{-1}	1
Relative tuber death rate (on number basis)	RDTU	0.026 d^{-1}	5
Initial Growth of Sprouts			
Relative conversion rate of tuber into plant material	ROC	0.0576 g CH_2O. g DW^{-1} d^{-1}	6
Relation coefficient tuber weight-stem length	RCSHST	12 m. g DW^{-1}	6,7,8
Critical shoot weight per depth layer	CRIFAC	0.0076 g DW. 0.1 m plant layer^{-1}	7,8
Survival period for sprouts without net photosynthesis	SURPER	27 d	1
Light, Photosynthesis, Maintenance, Growth and Assimilate Partitioning			
Water type specific light extinction coefficient	L	1.07 m^{-1}	1
Plant species specific light extinction coefficient	K	0.095 m^2 g DW^{-1}	1
Potential CO_2 assimilation rate at light saturation for shoot tips	AMX	0.019 g CO_2 g DW^{-1} h^{-1}	9
Initial light use efficiency for shoot tips	EE	0.000011 g CO2 J^{-1}	10
Reduction factor for AMX to account for senescence plant parts over vertical vegetation axis	REDF	1.0	user def.
Daytime temperature effect on AMX as function of DVS	AMTMPT*	0-1	1
Reduction factor to relate AMX to water pH	REDAM	1	1
Conversion factor for translocated dry matter into CH_2O	CVT	1.05	10
Dry matter allocation to each plant layer	DMPC*	0-1	1
Thickness per plant layer	TL	0.1 m	11
Water depth	DEPTH	1.3 m	user def.
Daily water temperature (field site)	WTMPT	-, °C	user def.
Total live dry weight measured (field site)	TGWMT	-, g DM m^{-2}	user def.

(Continued)

Table 2 (Concluded)

Parameter	Abbreviation	Value	Reference
Induction and Formation of New Tubers			
Translocation (part of net photosynthetic rate)	RTR	0.19	1, 12
Tuber number concurrently initiated per plant	NINTUB	8 plant^{-1}	1,8
Critical tuber weight	TWCTUB	19.92 g DW m^{-2}	1,4
Tuber density measured (field site)	NTMT	440 m^{-2}	4
Flowering and Senescence			
Relative death rate of leaves (on DW basis; Q_{10}=2)	RDRT	0.047 d^{-1}	1
Relative death rate of stems and roots (on DW basis; Q_{10}=2)	RDST	0.047 d^{-1}	1
Harvesting			
Harvesting	HAR	0 or 1	user def.
Harvesting day number	HARDAY	1-365	user def.
Harvesting depth (measured from water surface; 1-5 m)	HARDEP	0.1m<DEPTH	user def.

1. Appendix C; 2. Sher-Kaul et al. 1995; 3. Howard-Williams 1978; 4. Van Wijk 1989; 5. Van Wijk 1988; 6. Best and Boyd 1996; 7. Spencer 1987; 8. Spencer and Anderson 1987; 9. Van der Bijl et al. 1989; 10. Penning de Vries and Van Laar, 1982a, b; 11. Titus et al. 1975; 12. Van Wijk et al. 1988; *, Calibration function

4 Performance Tests

Simulated and Measured Behavior of a Sago Pondweed Community in the Western Canal near Zandvoort, The Netherlands

Nominal run

The seasonal changes in biomass of plant shoots and roots and of the tuber bank as simulated by POTAM are shown in Figure 6. Simulated plant biomass compared well with average plant biomass measured in the Western Canal near Zandvoort, The Netherlands (Appendix C). Plant biomass reached its maximum 13 days later, and peak biomass was somewhat higher in the simulated than in the measured plant community, notably 101.9 versus 78.5 g DW m^{-2}. However, the simulated biomass higher than measured biomass may be due to the use of air temperatures instead of the measured water temperatures used as input for this nominal run. Air temperatures with a lag period of 7 days (default) were used because the temperature of the water surrounding the majority of the plant shoots in summer was closer to the temperature of the air than to the temperature of the water filling the canals via upward seepage. Another explanation may be that actual maximum plant biomass occurred at the end of August, as found for the 2.5-m depth class (Appendix C); but since biomass was measured only once a month, the actual peak was missed.

Simulated transport of carbohydrates was substantial in the beginning of the growth season when upward carbohydrate remobilization from the tubers supports initial sprouting, but far higher after flowering when downward carbohydrate translocation from plant organs supports the filling of the tubers (Figure 7). Carbohydrate transport could be in the same range as net assimilation at the beginning and end of the growth season (Figures 7 and 8). Maintenance respiration was usually considerably lower than assimilation but could be in the same range of translocation just after flowering (Figure 8).

Running the model with 24-hr averaged air temperatures and a lag period of 7 days instead of with measured water temperatures as forcing variables yielded far higher assimilation (Figure 9) and plant biomass values than yielded by model runs on water temperatures. This can be explained by the fact that water temperatures in the Western Canal were far lower than air temperatures in summer, because of the large inflow of groundwater (Appendix C). In the

experience of the authors, a lag period of 7 days between model daily air and measured temperatures usually describes this relationship well for shallow water bodies, up to 5-6 m deep, without large inflows of groundwater. It has to be cautioned that the relationship between the temperatures of air and water body may differ, since temperatures within each water body are influenced by catchment morphometry, wind speed, fetch, mixing processes, and upward seepage. This example illustrates the usefulness of inclusion of both temperature options in the model, facilitating its operation by users who do not possess a full data set of water temperatures for the water body for which they desire to run the model.
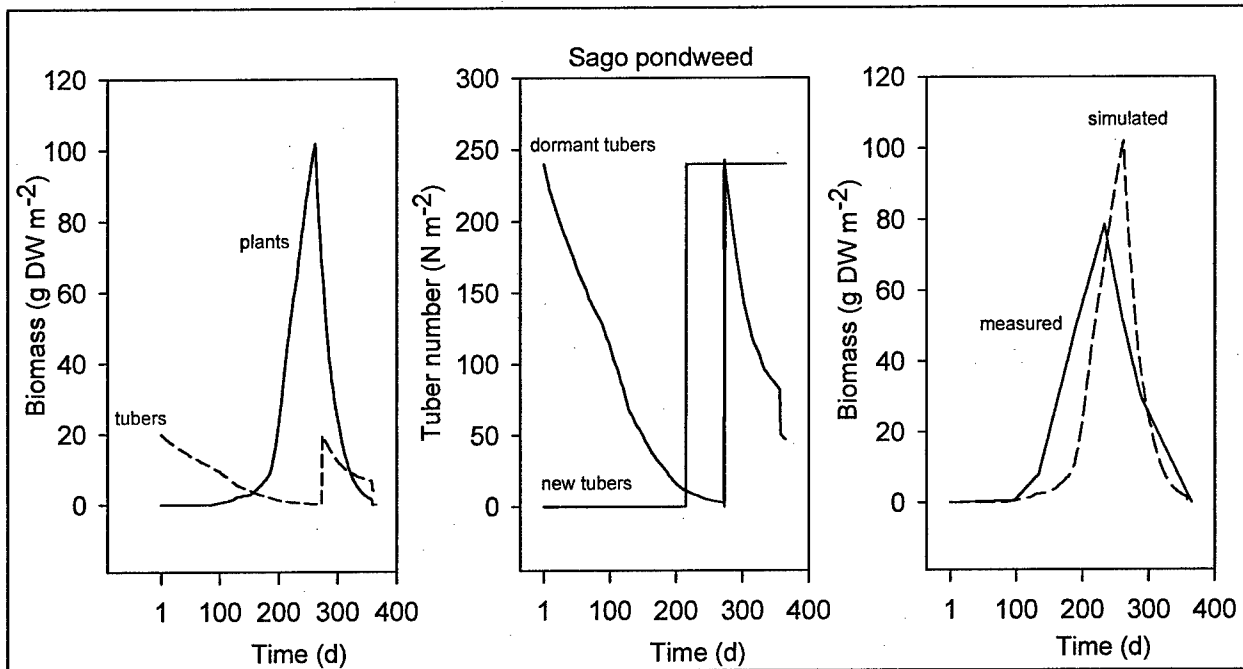
Figure 6. Simulated biomass of plants, dormant and new tuber numbers, and measured plant biomass of a sago pondweed community in the Western Canal near Zandvoort, The Netherlands. Nominal run. Field data from Appendix C; climatological data 1987, De Bilt, The Netherlands (longitude 05°11' E, latitude 52°06' N); water depth 1.3 m; light extinction coefficient 1.07 m^{-1}

Running the model for the same canal and year, but with both plants and tubers initially present, showed that peak plant biomass was greatly increased but no tuber class was finished (Figure 10b). The large increase in peak biomass is due to the ability of the plant community to fully capture the high spring irradiance at this latitude of 52° N, which they cannot without wintering shoots. However, since maintenance respiration increased proportionally to plant biomass and light extinction due to self-shading was high, carbohydrate reserves invested in tubers were insufficient to finalize a large sized tuber class; consequently, such plant population would become extinct the next year. Thus, wintering shoots would not provide a distinct advantage for this plant species in a temperate climate. A simulation started with initial plant biomass but from a smaller tuber size/concurrently initiated tuber number combination (a 0.07 g DW and 6 tubers

per plant) yielded a far higher peak plant biomass and 50 percent reduced tuber numbers compared to the values measured in the Western Canal (Appendix C).
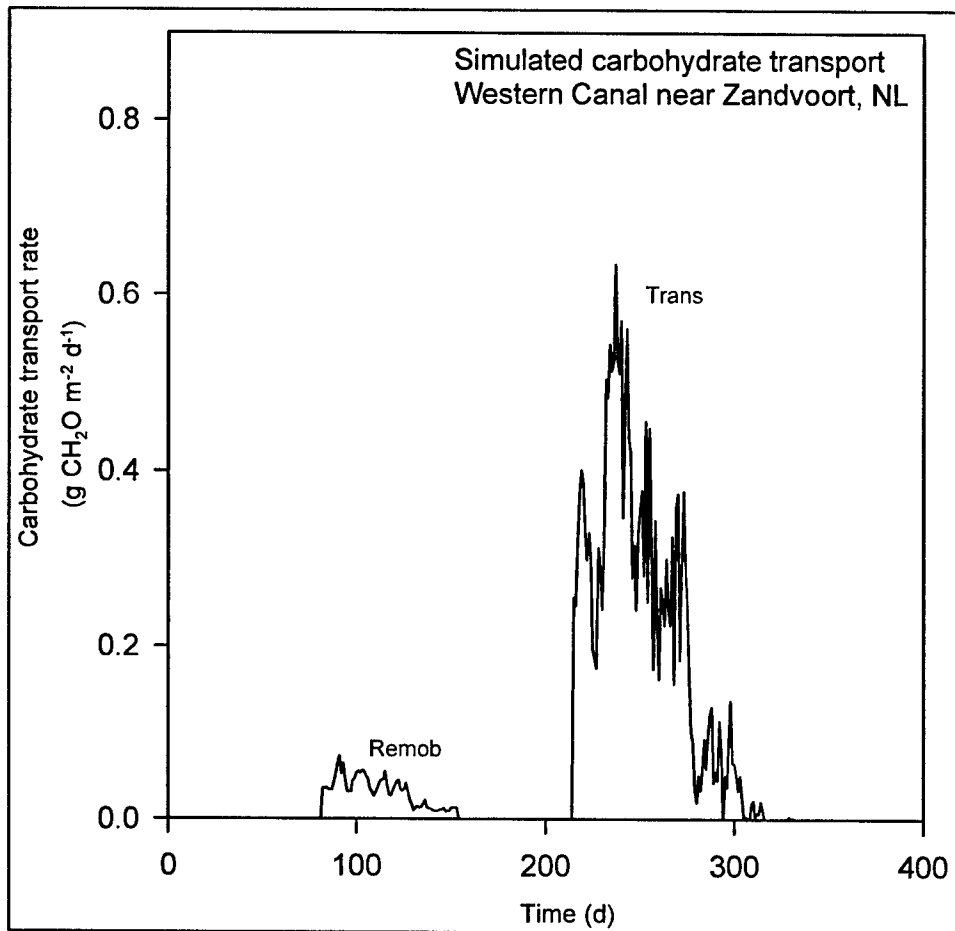
Figure 7.　Simulated behavior of carbohydrate flow through plant compartments of a sago pondweed community in the Western Canal near Zandvoort, The Netherlands (carbohydrate remobilization and upward transport from the tubers is used for initial growth of plants. Downward carbohydrate translocation into tubers occurs during anthesis and senescence (initial biomass and climatological data as in nominal run))

Effects of differences in leaf surface:dry weight ratio

A large range of leaf surface area:dry weight ratios (K-value) in sago pondweed has been found. All K-values were measured in sago pondweed populations in temperate climates, varying from 0.0183 m^2 g DW^{-1} by Sher-Kaul et al. (1995) in populations in mesotrophic Lake Geneva, Switzerland, to 0.02 m^2 g DW^{-1} by Westlake (1964) in British calcareous stream populations, to 0.095 m^2 g $AFDW^{-1}$ in a population in the eutrophic Western Canal, The Netherlands (Appendix C). It is possible that sago pondweed populations in a tropical climate may have thinner leaves, with a concomitant lower K-value, as was found in american wildcelery in Australia (0.051 m^2 g DW^{-1}; Blanch et al. 1998) and in

Eurasian watermilfoil (Best and Boyd 1999), but to the knowledge of the authors no such K-value has been published yet.
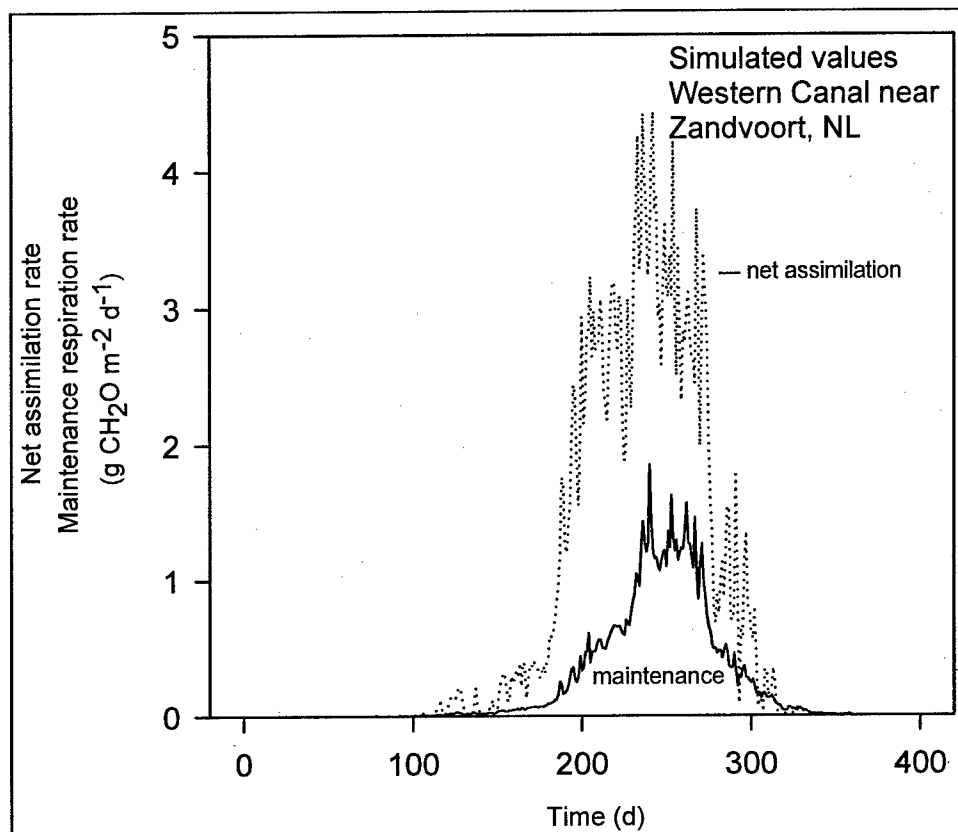
Figure 8. Simulated rates of daily net assimilation and maintenance respiration of a sago pondweed community in the Western Canal near Zandvoort, The Netherlands (initial plant parameter values as in nominal run)

Simulations indicated that peak plant biomass increased with decreasing K-value to a small extent but not proportionally, and that tuber production was similar (Figure 11). A sago pondweed community starting from the same tuber bank as the nominal one and characterized by a K-value of 0.020 m^2 g DW^{-1} (compared to the nominal value of 0.095 m^2 g DW^{-1}) would produce about 13 percent more biomass than a nominal community. Plant biomass and tuber production were similar for communities with K-values of 0.020 and 0.0183 m^2 g DW^{-1} (Figure 11).

Effects of differences in tuber bank density and anchorage depth

Sago pondweed has shown the ability to colonize shallow aquatic areas rapidly because it may form various diaspores, among which tubers are the most numerous (Yeo 1965). To explore the potential for rapid population establishment from only a few tubers, the model was run from an initial tuber bank density of 10 tubers m^{-2} under nominal climatological conditions at a higher than nominal anchorage depth, i.e., 2.5 m. It turned out that under these conditions substantial plant biomass was formed and that one more tuber class was finished than in a nominal population (Figure12B versus Figure12A), probably because less self-

shading occurred. However, a population starting from a nominal tuber bank density of 240 tubers m^{-2} at a greater anchorage depth of 5 m would become extinct within a year (Figure12C), due to the greater light extinction within the higher water column. Tuber size turned out to be more important than tuber bank density, since plantlets emerging from smaller tubers tended to die before attaining a self-supporting carbon-gain level.
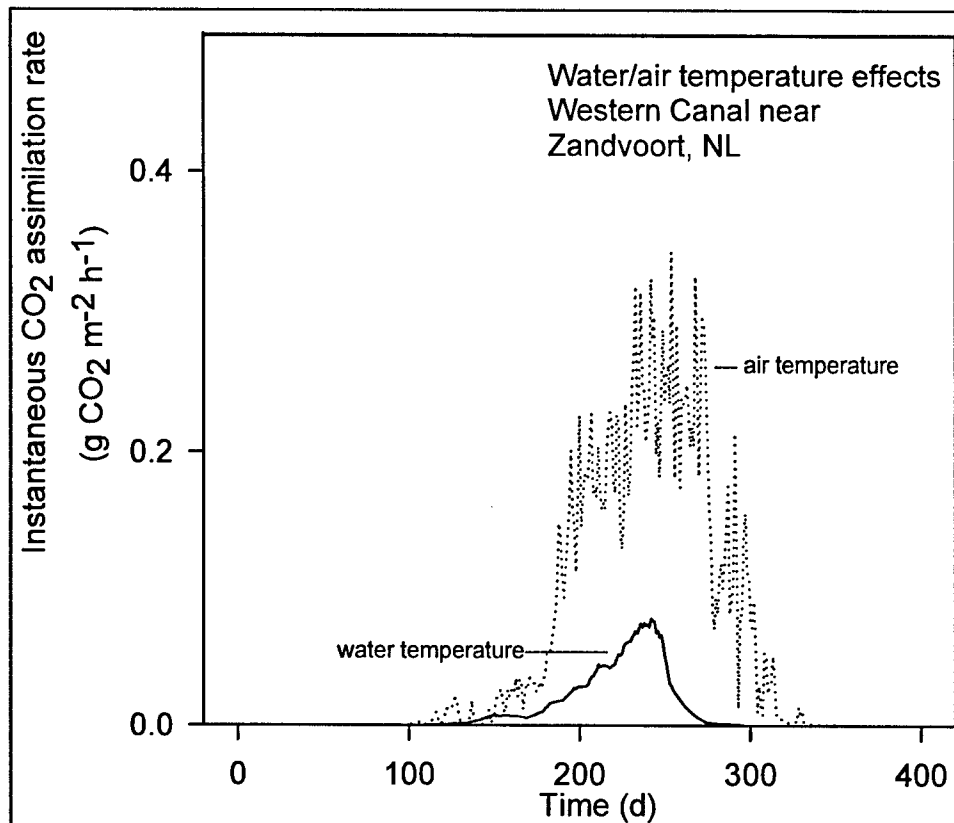
Figure 9. Simulated photosynthetic rates of a sago pondweed community in the Western Canal near Zandvoort, The Netherlands, with water or air temperatures as input (initial plant parameter values as in nominal run)

Simulated and Measured Behavior of a Sago Pondweed Community in Lake Veluwe, The Netherlands, in Two Consecutive Years with Greatly Different Turbidities

Lake Veluwe, located in the center of The Netherlands, is a man-made, shallow, wind-exposed, eutrophic lake in which remnants of sago pondweed populations remained at the end of the 1970s (Bick and Van Schaik 1980). The decline in aquatic macrophyte coverage area was attributed to increased turbidity due to eutrophication, and management strategies were sought to reverse this decline. Management including regularly flushing the lake and a reduction in external phosphorus loading resulted in a more transparent water column and a slow increase in the area colonized by sago pondweed. Because this management

scenario did not lead to a full recovery of the sago pondweed population, several studies have been undertaken to quantify the relationship between light availability within the water column and the production of plant biomass and tubers in this lake. Field data on plant and tuber biomass, and on local water transparency generated by the studies mentioned previously have been used to validate the data simulated using POTAM (Van Dijk et al. 1992; Van Dijk and Achterberg 1992).
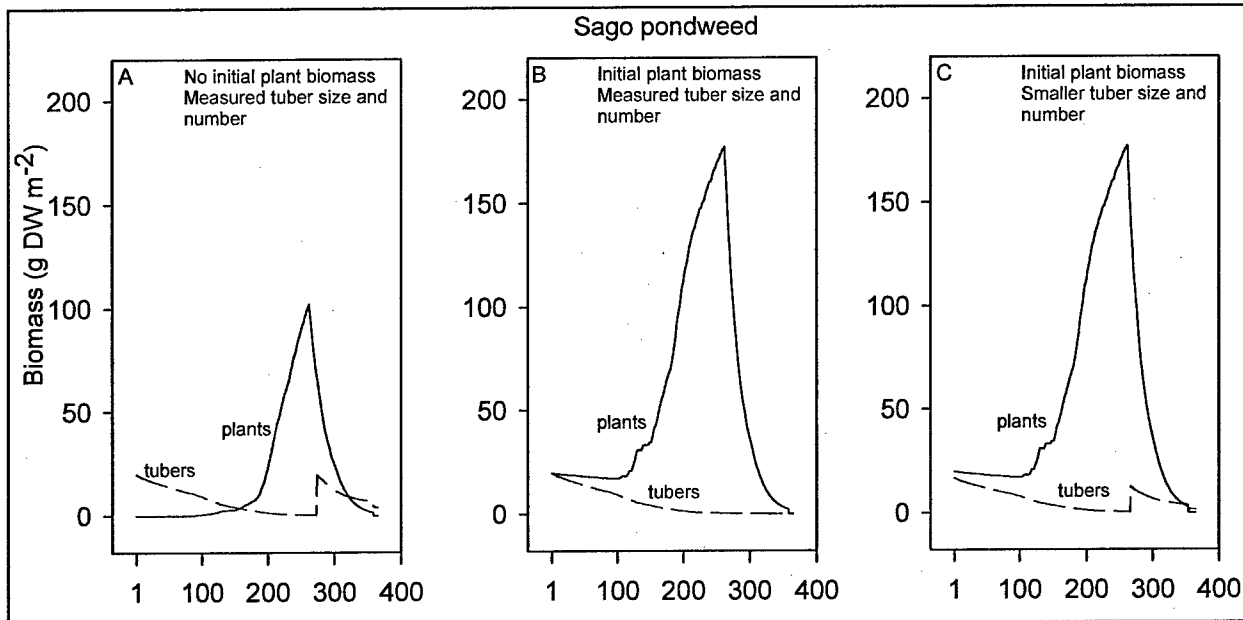
Figure 10. Simulated biomass of plants and tubers of a sago pondweed community in the Western Canal near Zandvoort, The Netherlands, started from different initial biomass conditions, but run in the same environmental and climatological nominal conditions: (A) Plant biomass 0; tuber size 0.083 g DW; tuber bank 240 m^{-2}, (B) Plant biomass 20 g DW m^{-2}; tuber size 0.083 g DW; tuber bank density 240 m^{-2}; (C) Plant biomass 20 g DW m^{-2}; tuber size 0.070 g DW; tuber bank density 240 m^{-2}

The model was run for two consecutive years greatly differing in turbidity, i.e., 1986 and 1987, using as initial values the measured tuber bank densities and predominant tuber sizes. Model results indicated that a higher plant biomass but lower tuber class number (four classes in 1986 versus seven classes in 1987) would be expected in 1986 than in 1987, with plant biomass and newly produced tuber densities similar to measured ones (Figure 13). The timing at which the simulated maxima in plant biomass and tuber density occurred coincided with the measured values in 1986, but were delayed in 1987 (Figure 13). This example illustrates that although intuitively it would be expected that a larger peak plant biomass would lead to a higher tuber density, it is possible that in reality fewer tubers are formed since the latter process does not depend only on plant biomass but also on the critical combination of day length and temperature.
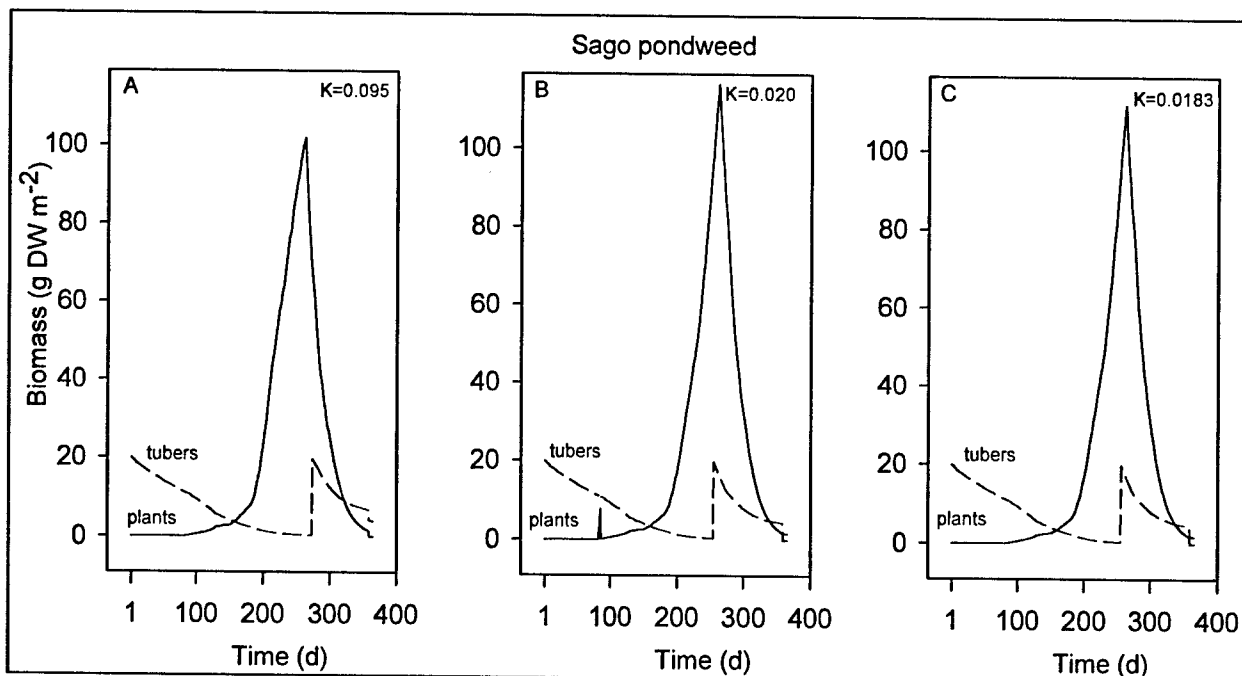
Figure 11. Simulated biomass of plants and tubers of a sago pondweed community in the Western Canal near Zandvoort, The Netherlands, started from identical nominal initial biomass conditions, except for the K-value (climatological data as in nominal run). K-values of (A) 0.095 m^2 g AFDW^{-1} (Appendix C); (B) 0.020 m^2 g DW^{-1}; Westlake (1964; as used by Hootsmans 1991) ; (C) 0.0183 m^2 g DW^{-1}; Sher-Kaul et al. (1995)
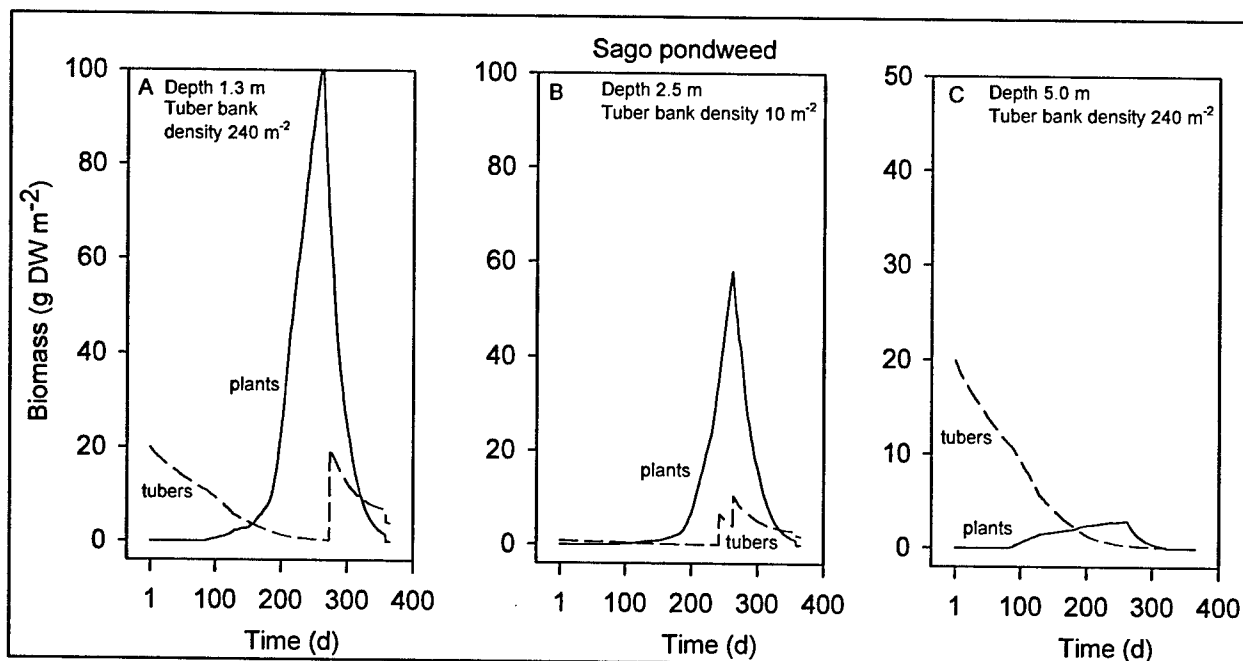
Figure 12. Simulated biomass of plants and dormant tubers of a sago pondweed community in the Western Canal near Zandvoort, The Netherlands, started from nominal initial biomass data differing in tuber bank density and anchorage depth (climatological data as in nominal run). (A) Tuber size 0.083 g DW, tuber bank density 240 m^{-2}; rooting depth 1.3 m; (B) Tuber size 0.083 g DW, tuber bank density 10 m^{-2}; rooting depth 2.5 m; (C) Tuber size 0.083 g DW, tuber bank density 240 m^{-2}; rooting depth 5.0 m
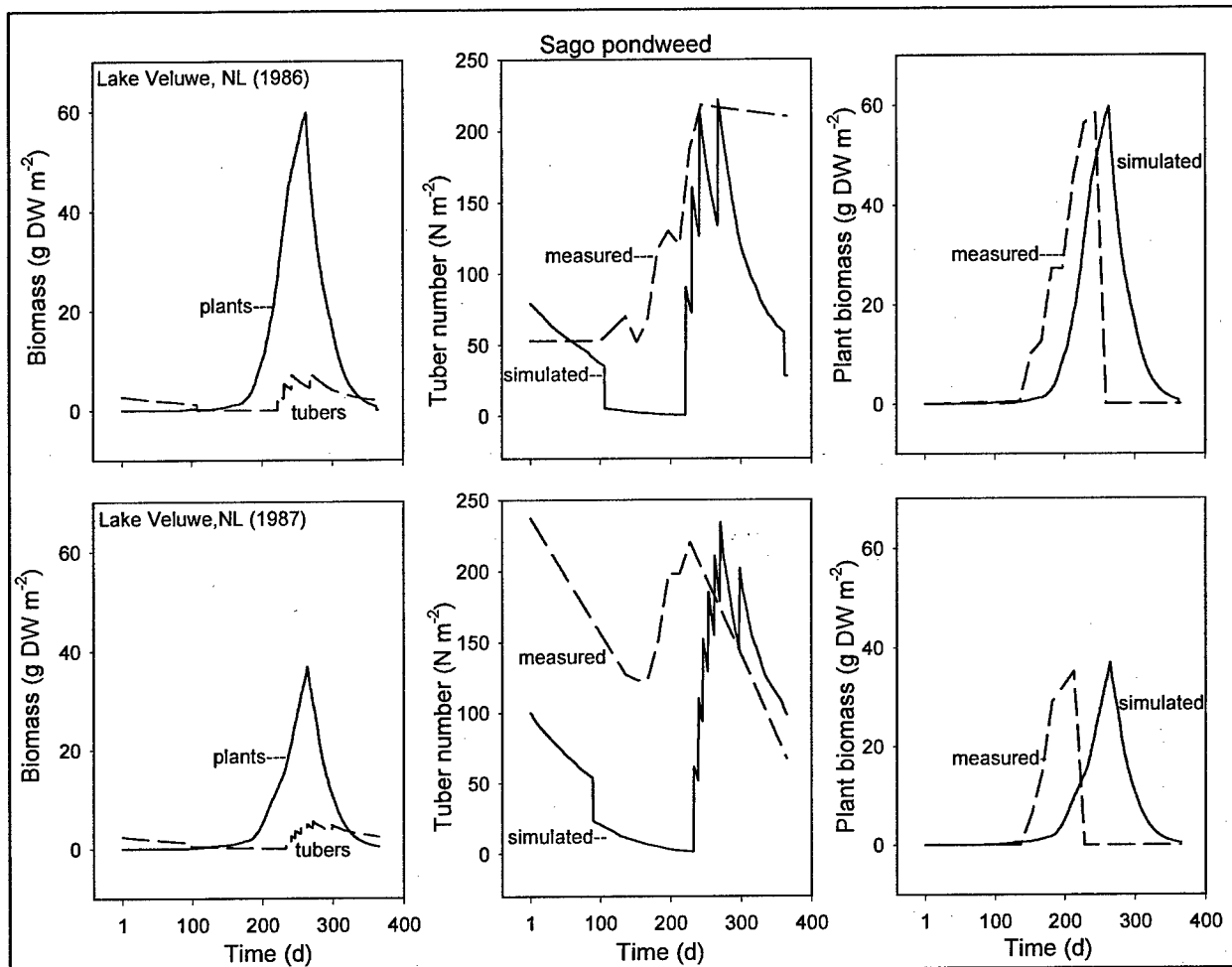
Figure 13. Simulated and measured biomass of plants and tubers of sago pondweed in Lake Veluwe, The Netherlands, during two successive years differing in water transparency. Initial values on tuber size and tuber bank density from Van Dijk et al. 1992; 1986, initial tuber weight 0.034 g dry weight, tuber bank density 79 m^{-2}, water depth 0.5 m; 1987, initial tuber weight 0.024 g dry weight, tuber bank density 100 m^{-2}, water depth 0.5 m. Light extinction coefficient from Van Dijk and Achterberg 1992; 1986, average May-September 2.58 m^{-1}; 1987, average 4.30 m^{-1}. Climatological data 1986, 1987, De Bilt, The Netherlands (longitude 05°11' E, latitude 52°06' N)

Simulated and Measured Behavior of a Sago Pondweed Community at Other Latitudes

To investigate whether the model is able to simulate the behavior of a sago pondweed community at other sites besides the nominal one, runs were made for two other sites, one more western, the Byrnes Canal, California, and one more southern, tropical Lake Ramgarh, India.

A simulation was performed of a sago pondweed community in the Byrnes Canal, California, starting from site-specific community, water depth, transparency, and climatological data. For this site, plant community-specific data included the following:

a. Initial plant biomass: absent.

b. Tuber size: 0.025 g DW.

c. Concurrently initiated tuber number: 3 plant^{-1}.

d. Tuber bank density: 700 m^{-2}.

The following environmental data were included:

a. Water depth: 0.2 m.

b. Light extinction coefficient: 0.4 m^{-1}.

In these conditions, simulated plant biomass showed a maximum of 130 g DW m^{-2} using the nominal self-shading coefficient (KT) of 0.095 m^2 g DW^{-1}, but a maximum close to the measured biomass of 175 g DW m^{-2} at a lower self-shading coefficient of 0.0183 m^2 g DW^{-1} (as reported by Sher-Kaul et al., 1995, for clear Lake Geneva. In both simulations many tuber classes were finished, giving rise to extremely high tuber densities just as found in situ (Figure 14B; Spencer 1990, unpublished results[1]).
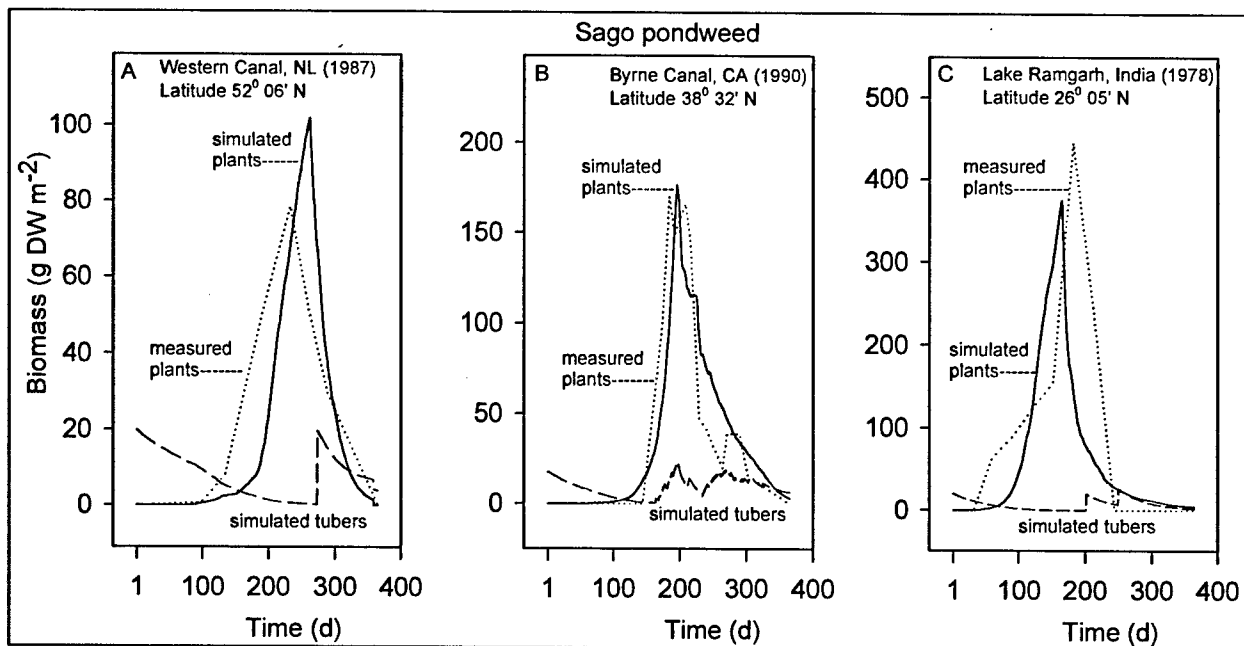
Figure 14.   Simulated biomass of plants and tubers of a sago pondweed community at sites differing in latitude. (A) The Western Canal near Zandvoort, The Netherlands (longitude 05°11' E, latitude 52°06' N; tuber size 0.083 g DW, tuber bank density 240 m^{-2}; water depth 1.3 m; light extinction coefficient 1.07 m^{-1}; climatological data 1987; validation data 1987 (Appendix C). (B) Byrne Canal, CA (longitude 121°47' W, latitude 38°32' N; tuber size 0.025 g DW, tuber bank density 700 m^{-2}; K-value 0.0183 m^2 g DW^{-1}; water depth 0.2 m; light extinction coefficient 0.4 m^{-1}; climatological data 1990; validation data 1990, Spencer[1]). (C) Lake Ramgarh, India (longitude 83°26' E, latitude 26°05' N; tuber size 0.083 g DW, tuber bank density 240 m^{-2}; K-value 0.0183 m^2 g DW^{-1}; water depth 1.3 m; light extinction coefficient 1.07 m^{-1}; climatological data Patancheru, India, 1978 (longitude 78°28' E, latitude 17°27' N); validation data 1968, Sahai and Sinha (1973)

[1] Dr. David Spencer, U.S. Department of Agriculture – Agricultural Research Service, University of California, Davis, December 2001.

Another simulation was performed of a sago pondweed community in Lake Ramgarh, India, starting from a nominal community, water depth, and transparency, with climatological data pertaining to Patancheru, India. For this site, plant community-specific data included the following:

a. No initial plant biomass.

b. Tuber size: 0.083 g DW.

c. Concurrently initiated tuber number: 8 plant^{-1}.

d. A tuber bank density of 240 m^{-2}.

In these conditions simulated plant biomass was high, maximally 375 g DW m^{-2}, and only two tuber classes could be finished within a year. Tuber weights and numbers of the Lake Ramgarh community were not published, so comparison between simulated and measured tuber data is not possible. However, simulated maximum plant biomass in this case was in the same order of magnitude as the measured peak biomass of 445 g DW m^{-2} (Figure 14C).

Comparison of biomass production characteristics in the various climatological conditions (Figure 14) indicates that in a temperate climate generally less biomass is produced, but investment in vegetative reproduction is relatively higher than in a tropical climate. The criteria for tuber formation, (a) timed just after flowering, (b) day length between 12 and 16 hr, and (c) temperature between 5.5 and 25 °C, were met for long continuous periods in The Netherlands and California, but only occasionally in India because the temperature usually exceeded the critical range. In The Netherlands tubers could be initiated from day 215 to 250 at relatively moderate irradiance, allowing only one tuber class to be finished (Figure 15A); in California tubers could be initiated from day 161 to 250 at far higher irradiance, giving rise to many tuber classes (Figure15B); in India tubers could be initiated from day 150 to 220 so that only two tuber classes might be finished (Figure 15C). The extremely limited window for tuber formation in tropical regions was confirmed recently by Pilon (1999), who reported that the number of tubers formed per plant increases from around 0 at a latitude of 25 °N to 8 at 68 °N, but predominant tuber size decreases from 0.022 to 0.006 g DW tuber^{-1}. Although the latter characteristics were suggested at first to have a genetic basis, it was reported later on that they may be environmentally regulated (Pilon and Santamaria 2002). This example illustrates the usefulness of inclusion of phenology tied to degree-day sum in the model, allowing it to perform simulations for different sites and climates. This feature facilitates its operation by users who do not possess a full data set on plant characteristics and environmental variables for the water body for which they desire to run the model.

The tentative difference in importance of sexual reproduction between climates cannot be explored with the current version of the model, since sexual reproduction has not been included.
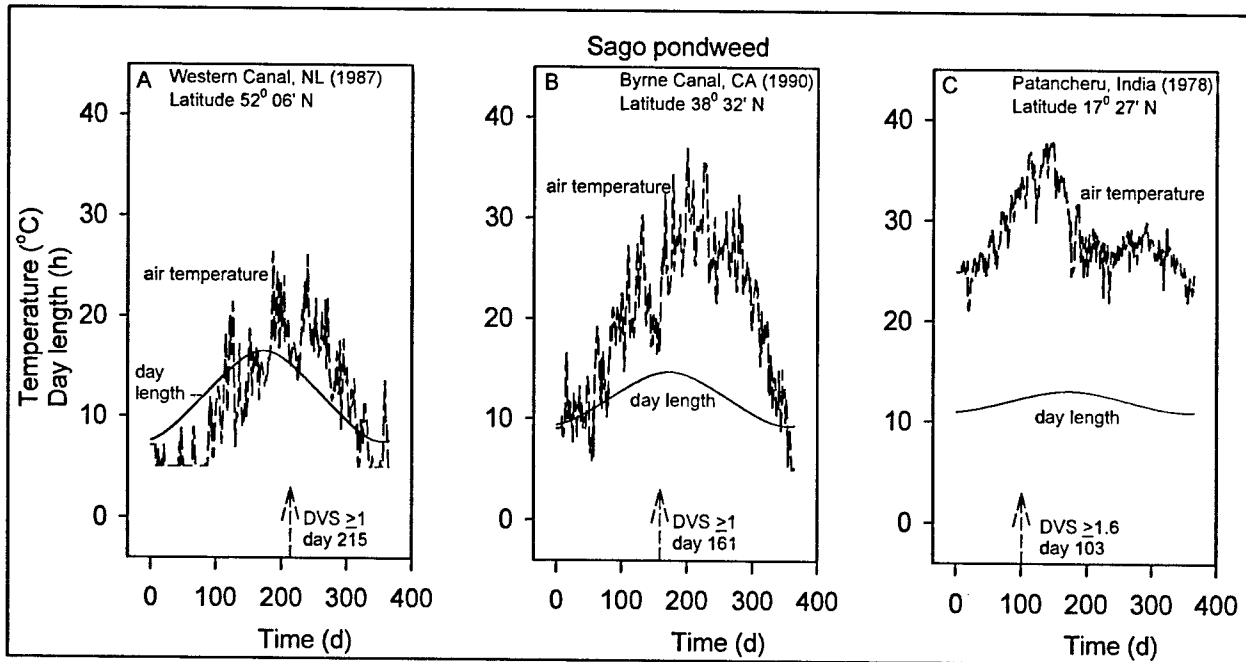
Figure 15. Developmental stage and Julian day number at which tuber formation is initiated in a sago pondweed community at sites differing in latitude, in relation to day length and temperature. (A) The Western Canal near Zandvoort, The Netherlands (longitude 05°11' E, latitude 52°06' N; climatological data 198). (B) Byrne Canal, CA (longitude 121°47' W, latitude 38°32' N; climatological data 1990). (C) Patancheru, India 1978 (longitude 78°28' E, latitude 17°27' N; climatological data 1978)

Historical and Simulated Behavior of a Sago Pondweed Community in a Riverine Environment Subject to Flooding

Sago pondweed is an important riverine macrophyte that provides food and habitat resources for waterfowl, fish, and invertebrates in the Upper Mississippi River (UMR). Navigation pools along the Mississippi Flyway have historically been used by migrating waterfowl as staging areas in part because of abundant populations of tuber-producing aquatic macrophytes (Bellrose et al. 1983; Korschgen et al. 1988; Korschgen 1989). Declines in the populations of tuber-producing aquatic macrophytes, such as American wildcelery and sago pondweed, have occurred since 1988, and continued through the 1990's (Green 1960; Fischer and Claflin 1992). These declines have been attributed to eutrophication, sediment nutrient depletion, competition by other macrophytes such as Eurasian watermilfoil (*Myriophyllum spicatum* L.) and American lotus (*Nelumbo lutea* (Willd.) Pers.) in shallow areas, drought, flooding, and changes in current velocity and wave characteristics as consequences of increased navigation (Rogers 1996). It is desirable to improve management programs aimed at enhancing tuber-producing macrophyte populations, but these programs require an improved understanding of the population dynamics of these plants and factors affecting them.

Simulations were carried out to evaluate the effects of daily changes in water level during different hydrological years on a typical sago pondweed community in Pool 8 of the UMR. Stage data collected at the dam of Pool 8 were used to document water level fluctuations over a 10-year period, from 1985 to 1994. In this period, 1985 is considered as a normal hydrological year, 1986 as a normal flood year with floods in spring and autumn, 1993 as an abnormal flood year with one flood in summer, and 1988 as a drought year (Figure 16).

The simulations were done starting from a nominal sago pondweed community, site-specific environmental data, and site- and year-specific climatological data. Site-specific environmental data included water depth daily varying as would be experienced by a community at 0.5-m anchorage depth; and a light extinction coefficient ranging from 2.619 to 3.173 m^{-1} during May to October, and set to 2.0 m^{-1} the rest of the year (converted via Giesen's relationship from Secchi disk readings (Giesen et al. 1990) correlated with 10-year data on total suspended solids concentrations). Since no historical data on biomass were available, only comparison with presence/absence documentation was possible (Figure 17C).

Running POTAM with nominal initial plant biomass and tuber bank data at a constant 0.5-m water depth with a 10-year average climate indicated that a peak biomass of 105 g DW m^{-2} was formed, and that two tuber classes would be finished. Under the same conditions, a 2-m depth class would produce 72 g DW m^{-2} and only one tuber class (Figure 17B). Water fluctuations were usually substantial, and it was therefore concluded that calculation of the annual average water depth from nine historical data might yield an erroneous, probably too high, average and that, therefore, the simulated plant biomass would be an underestimate. As expected, more plant biomass (20 percent) would be produced, but only one tuber class finished, under a normal water level fluctuation regime in Pool 8, pointing to a tentative positive influence of relatively small water level fluctuations as found in 1985 (Figure 17C). Normal flooding inhibited biomass and tuber production somewhat, but allowed two tuber classes to be finished possibly because the midsummer water levels were somewhat lower than in 1985 (Figure 17D). The relatively small size of this effect was attributed to the fortuitous timing of the high water levels that occurred only in spring and autumn, still allowing the plants to fully benefit from the high summer irradiance at normal water levels. Abnormal flooding, however, reduced the finished number of tuber classes by a factor of 2 in the 0.5-m depth class (Figure 17E), and completely prevented tuber formation in the 1-m depth class (latter data not shown). The harshness of this effect was attributed to the fact that the plants could not fully benefit from the high summer irradiance due to the high summer water levels. The effect of the 1988 drought was surprising. In this year substantial plant biomass could be produced peaking relatively early in the growth season, but tuber formation was inhibited later on—as in the case of abnormal flooding—because (a) water levels were kept relatively high later in summer, possibly as a water conservation measure, causing increased extinction of light within the water column, and (b) temperatures were relatively high, causing increased respiration and senescence. The increased light extinction in the water column may even have been larger in situ than in the simulation, since during droughts not only water levels may change but also extinction within the water column may increase by
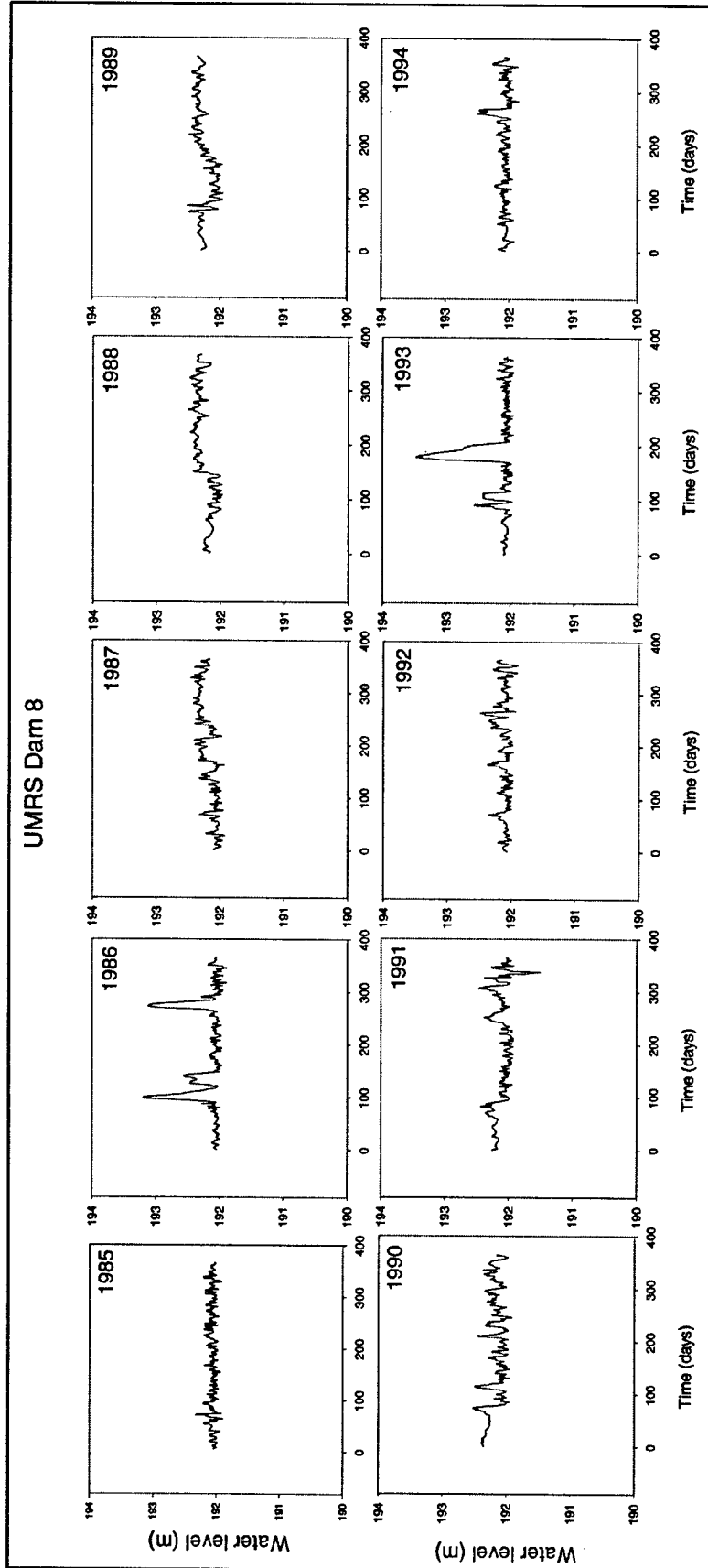
Figure 16. Water level fluctuations over a 10-year period measured at the dam of Pool 8 of the Upper Mississippi River, Wisconsin (data J. H. Wlosinski, La Crosse, WI, December 2001). Flat pool is considered to be the average summer (June, July, August) value during normal hydrological years over the 1985-94 period; abnormal hydrological years were 1986, 1988, and 1993
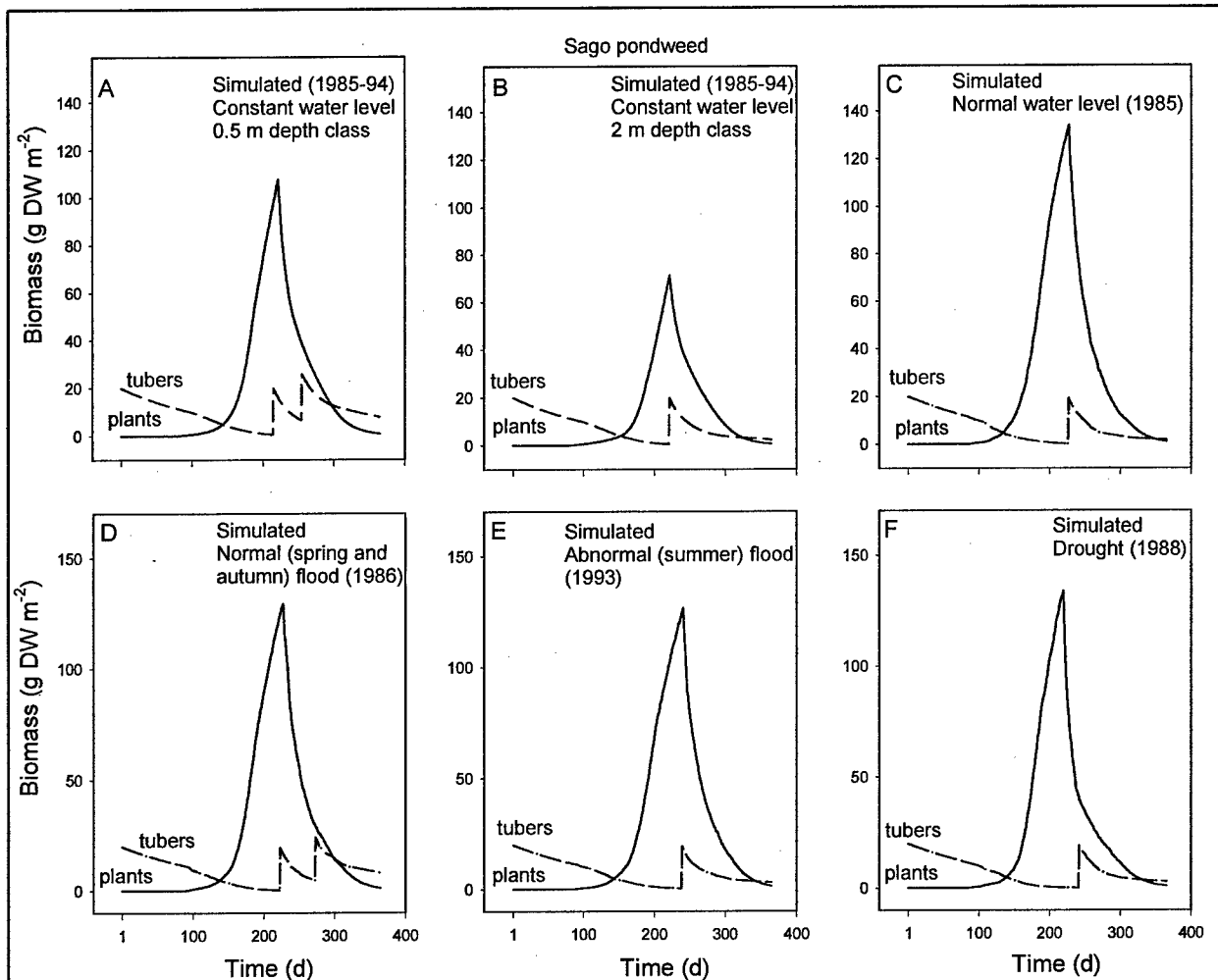
Figure 17. Comparison of simulated data on biomass of plants and tubers of sago pondweed in the Upper Mississippi River. Historical data on macrophyte occurrence in Pool 8 (longitude 91°30' W, latitude 43°30' N) during the period 1993-98[1] used as a reference. Simulations: Nominal initial biomass data; light extinction coefficients derived from 10-year average background total suspended solids values measured in the nearby Pool 4 in the 1980's (Bartell et al. 2000); climatological data, Minneapolis/St. Paul, Minnesota (longitude 93° W, latitude 45° N). (A) and (B) Constant water levels; climate, average 1985-94; (C) Water level, daily values 0.5-m depth class; climate 1985; (D) Water level, daily values 0.5-m depth class; climate, 1986; (E) Water level, daily values 0.5-m depth class; climate 1993; (F) Water level, daily values 0.5-m depth class; climate, 1988

[1] Personal Communication, December 2000, Y. Yin, U.S. Geological Survey, Upper Midwest Environmental Sciences Center, La Crosse, WI.

stimulation of algal blooms. The seasonal changes in the light extinction coefficient were kept the same in all simulations.

This example illustrates how relatively low- and high-frequency fluctuations in water levels might affect submersed plant populations, without even taking plant adaptation into consideration. Ability of plants to adapt to changes in water level may be an important characteristic for their persistence in rivers, reservoirs, and estuaries. Although this ability is a rather intensively discussed research topic, pertinent ecological data are currently largely lacking. The field observations indicating large portions of sago pondweed populations disappeared after the 1988 drought (Green 1960) and 1993 unusual flood (Spink and Rogers 1996) may be explained by desiccation of tubers in shallow areas that fell dry, and dislodgement of tubers in areas exposed to unusual current velocities, both phenomena not described in the current POTAM model.

Simulated Behavior of a Sago Pondweed Community Subject to Biomass Removal; Effects of Cutting and Grazing

Effects of such man-made control activities as cutting at different times and at various water depths can be calculated also using POTAM. These control measures may be needed to free irrigation canals, such as those in agricultural areas in California, from obstructing aquatic weeds. Thus, in the latter case the model can be used as a tool by aquatic plant and lake management agencies.

Table 3
Effects of Cutting Date and Depth on Maximum Shoot Biomass and End-of-Year Tuber Number

Harvest Time	Harvest Depth m	Live Shoot Biomass 14 July g DW m^{-2}	Preharvest Shoot Biomass g DW m^{-2}	Postharvest Shoot Biomass g DW m^{-2}	End-of-year Tuber Number N m^{-2}
Initial plant biomass 0					
None		144.4			189
1 April	0.8	109.8	0.6	0.2	119
1 June	0.8	14.1	15.0	1.5	2
1 July	0.8	9.2	72.0	7.1	0
----------	0.1	133.4	72.0	68.7	234
1 August	0.8	144.4	96.3	9.0	0
1 September	0.8	144.4	57.4	5.5	0

Note: Results were obtained in a one-year simulation under Davis, California, 1990, conditions, starting from tubers alone, 0.025 g DW initial tuber size, a tuber bank density of 700 m^{-2}; K-value 0.0183 m^2 g DW^{-1}; water depth 1.0 m; light extinction coefficient 0.4 m^{-1}

From Table 3 it can be concluded that sago pondweed vegetation at a 1-m anchorage depth starting from tubers alone does not produce such a high "nuisance" plant biomass in a relatively warm, temperate climate that it would hamper other uses of the water body by humans or wildlife, since peak plant biomass would not exceed 145 g DW m^{-2}. A cutting regime aimed at reducing

summer plant biomass concomitant with preventing tubers to be present at the end of the year would be most successful when implemented in the period between 1 June and 1 July with a cutting depth of 0.8 m (Table 3). Cutting to a lesser depth of 0.1 m in the same period would increase the end-of-year tuber number significantly by decreasing the self-shading effect of the plant canopy and, thus, allowing more light to reach the remaining plant portion. Since in a temperate climate usually no wintering plants are present, no simulations starting from biomass other than tubers were done. The same cutting regime applied to vegetation at a 0.5-m anchorage depth indicated that in this case expected peak biomass would be about 50 percent higher. A small drawback of the model in simulating cutting effects is that the model allows the simulated plant material that remains after harvesting to be distributed directly (i.e., during the next time-step) over the water column again, resulting in a slightly higher peak biomass, while in reality the vegetation will need more time to recover from cutting.

Sago pondweed fruits, seeds, and tubers form an important food source largely for waterfowl, but also for mammals such as muskrat, beaver, and moose, and for fish (Fassett 1957; Dirksen 1982; Van Wijk 1988; Korschgen 1989; Kantrud 1990). Waterfowl species commonly grazing sago pondweed in the United States are diving ducks (*Ayhtyinae*), dabbling ducks, and geese (*Anserinae*). Waterfowl species grazing this plant in European waters are mostly coot (*Fulica atra* L.), less frequently mallard (*Anas platyrhynchos* L.), and swans. Studies carried out to quantify the effects of waterfowl grazing on sago pondweed populations list mostly short-term effects varying from reductions in mass ranging from 40 to 83 percent for plants and from 43 to 66 percent for turions and tubers (Anderson and Low 1976; Van Wijk 1988). Longer-term, > 1 year, effects are believed to be small to negligible (Sterling 1970; Anderson and Low 1976; Kantrud 1986). The reported effects concur with the model results described in the section "Effects of differences in tuber bank density and anchorage depth," where a population starting from a lower tuber bank density than normal would completely recover within a year due to decreased self-shading. However, simulations starting from small tubers under relatively warm climatological conditions, such as occurring in California (<30 m^{-2}), indicated that populations starting from a lower than nominal tuber bank density would become extinct within a year. The latter phenomenon may be explained by the temperature-increased respiration of the sprouts emerging from the tubers, causing carbohydrate depletion before the plantlets attain a self-supporting carbon gain level.

The current Version 1.0 of POTAM can be used as a tool to estimate the viable forage habitat for waterfowl by calculating the timing and tuber size and density for sago pondweed populations at various sites with and without fluctuating water level, and at various anchorage depths. When made spatially explicit by interfacing with a Geographic Information System (GIS), POTAM can be used as the main tool in calculating viable habitats for these birds and other animals.

5 Sensitivity Analysis

A sensitivity analysis of a simulation model is required to assess the parameters likely to strongly affect model behavior. The current analysis was based on the effect of a change in a parameter when all other parameters are kept the same. As reference level, the nominal parameter values were chosen as presented in Table 2, under conditions at the Western Canal, The Netherlands, at 1.3-m water depth. In a 1-year simulation starting with a tuber size of 0.083 g DW and a tuber bank density of 240 m^{-2}, the value of the parameter under study was changed. The results were compared with those of a nominal run. Each parameter was once increased by 20 percent and once decreased by 20 percent. The relative sensitivity (RS) of a parameter was then defined as the relative change in the variable on which the effect was tested divided by the relative change in the parameter (Ng and Loomis 1984). The effects of ten parameters on two variables, representing plant biomass aspects, were tested. A model variable is considered sensitive to a change in the value of a parameter at RS > 0.5 and < -0.5. The current sensitivity analysis was performed over a 1-year period.

$$RS = \frac{(yield_i - yield_r)/yield_r}{(param_i - param_r)/param_r} \tag{8}$$

where
  $yield_i$ = value at parameter value i;
  $yield_r$ = value at reference parameter value;
    $param_i$ and $param_r$ as above

Maximum plant biomass proved most sensitive to changes in potential CO_2 assimilation at light saturation for shoots, but not to changes in light use efficiency. It was also strongly affected by changes in pre-anthesis development rate. Maximum plant biomass proved to be insensitive to changes in the other parameters tested.

End-of-year tuber number was sensitive to seven out of the nine parameters tested (Table 4). Sensitivity was greatest to changes in pre-anthesis development rate, followed by changes in relative tuber growth rate, potential assimilation rate, light use efficiency, post-anthesis development rate, plant density, and relative death rate of the plants. End-of-year tuber number was insensitive to changes in individual tuber weight and relative conversion rate of tubers into plant material.

This illustrates the utmost importance of the tubers for local survival and biomass production of sago pondweed.

Table 4
Relative Sensitivity of Two Model Variables to Deviations in Parameter Values from Their Nominal Values as Presented in Table 2

Parameter Name	Parameter Value	Relative Sensitivity	
		Maximum Live Plant Biomass	End-of-Year Tuber Number
Potential CO_2 assimilation rate at light saturation for shoot tips	0.019		
	0.0228	1.720	-1.577
	0.0152	1.941	5
Light use efficiency	0.000011		
	0.000013	0.245	-0.832
	0.000008	0.324	-3.095
Relative death rate for leaves, stems and roots	0.047		
	0.0564	0	0
	0.0376	0	-2.931
Individual tuber weight	0.083		
	0.0996	0.246	0
	0.0664	0.341	0.192
Relative conversion rate of tubers into plant material	0.0576		
	0.069	0.092	0
	0.046	0.136	0
Relative tuber growth rate	0.19		
	0.228	-0.103	-2.153
	0.152	-0.102	5
Plant density	30		
	36	0.276	1.204
	24	0.346	1.140
Pre-anthesis development rate	0.015		
	0.018	-1.360	-3.363
	0.012	-0.913	4.914
Post-anthesis development rate	0.040		
	0.048	-0.392	-0.426
	0.032	-0.451	-3.123

Note: Results were obtained in a 1-year simulation under conditions at Western Canal, The Netherlands, 1987 conditions, starting from 240 tubers m^{-2}

Earlier or later flowering biotypes are suited to different environments. The effect of changes in flowering date can be tested with the model by varying the pre-anthesis development rate of the vegetation. Faster rates represent earlier biotypes, and slower rates later biotypes. This sensitivity analysis shows that a faster pre-anthesis development rate than the nominal one leads to a lower peak plant biomass and end-of-year tuber number, but a slower pre-anthesis development rate leads to a lower peak plant biomass and higher end-of-year tuber number. The decreased peak biomass and increased tuber number in the latter case may be due to the relatively longer period in summer in which tubers can be initiated at the cost of plant biomass formation. Faster pre-anthesis development

leads to a shorter growing season and less vegetative dry matter, incomplete light interception, and lower carbohydrate availability for organ formation. At the same time, however, the rate of organ formation increases but the period in which each organ is formed shortens. Changes in post-anthesis development rates did not affect peak plant biomass to a large extent, but a slower rate did decrease the end-of-year tuber number. The latter decrease may be due to the relatively shorter period in which tubers can be initiated determined by the development stage of the plants concomitant with the occurrence of suitable environmental conditions for tuber initiation.

As far as is known, no publications exist on what the temperature requirements of aquatic plants are to traverse development from anthesis to senesced state. However, differences in post-anthesis development rates for several wheat and rice cultivars are known to be small and have little effect on yield (Van Keulen 1976).

Intuitive prediction of aquatic plant biotype behavior under variable climatic conditions is hazardous. The current model shows promise in being able to reproduce some of the complex vegetation responses and may be useful in evaluating long-term implications of differences in development rate.

6 Environmental Factor Analysis

The impacts of various changes in environmental factors were assessed using the relative sensitivity of the affected variables as "measure." For this purpose, parameter changes were based on value ranges taken from literature, which sometimes differed more than 20 percent from the nominal parameter value given in Table 2.

Climate

Climate greatly affects plant species distribution, phenological cycle, and biomass production. POTAM can be used to calculate climate change effects on the chronological timing of the phenological events and on biomass production. It cannot be used to assess climate change effects on (a) plant species distribution, and (b) the phenological cycle itself since the phenological cycle has been used for calibration (see Chapter 3). Running the model under more southern climatological conditions, i.e., changing the latitude from 52 to 38° N, demonstrated that both maximum plant biomass and end-of-year tuber number are sensitive to this climate change (Table 5).

Light Reflection Coefficient by Water Surface

The irradiance reflected by the water surface usually averages about 6 percent over a day. The values of this parameter tested were 0 and 1. Reflection may theoretically have the value 0 when no reflection occurs at a 90-deg incoming angle of the radiation on a completely calm water surface (wind and wave action are minimal). The highest value of 1 may occur at a close to 180-deg incoming angle of the radiation and at very rough water surfaces.

Increasing the light reflection coefficient to 1 brought plant biomass back to zero within the year. That nevertheless low RS values were found (Table 5) is an artifact of the calculation method employed. Decreasing the light reflection coefficient barely affected maximum biomass and end-of-year tubers, probably because the majority of the plant material is located at the water surface (Table 5).

**Table 5
Environmental Factor Analysis, Expressed as Relative Sensitivity
of Two Model Variables to Deviations in Parameter Values from
Their Nominal Values as Presented in Table 2**

| Parameter Name | Parameter Value | Relative Sensitivity | |
		Maximum Live Plant Biomass	End-of-Year Tuber Number
Climate			
Zandvoort, NL (1987)	Latitude 52° N	-	-
Davis, CA (1990)	Latitude 38° N	-1.540	1.425
Light reflection coefficient by water surface	0.06	0	-
	1.00 (+1567 percent)	-0.063	-0.063
	0.00* (-100 percent)	-0.016	0.085
Light extinction coefficient water column	1.07		
	1.284 (+20 percent)	-0.122	0.181
	0.856 (-20 percent)	-0.084	0.426
Water depth	1.3		
	1.56 (+20 percent)	-0.019	0
	1.04 (-20 percent)	0.034	0

Note: To enable calculation of the RS, a very low value of 0.000001 was used.
Results were obtained in a 1-year simulation under conditions at Western Canal, The Netherlands, 1987, starting from 240 tubers m^{-2}.

Light Extinction Coefficient of Water Column

A light extinction coefficient of on average 1.07 m^{-1} is used for nominal runs of the model (Western Canal, The Netherlands).

Changing the light extinction coefficient of the water column demonstrated small effects on maximum plant and larger effects on the end-of-year tuber numbers. A nominal value of 2 m^{-1} has been found typical for eutrophic fen lakes where submersed vegetation can just persist (Best et al. 1985).

Water Depth

POTAM has been calibrated for a water depth of 1.3 m, the anchorage depth of an extensively studied sago pondweed community in the Western Canal, The Netherlands. The model has the capability to respond to fluctuations in water level between years and within year, by (re)distributing plant biomass over the desired water depth (number of water layers; see Chapter 3). This technique for biomass distribution over the vertical axis of the community works well and gives realistic outcomes over a depth range of 0.1 to 6 m.

Running POTAM at an increased or decreased water depth showed negligible effects on maximum plant biomass and end-of-year tuber number, probably because the majority of the plant material is located at the water surface (Table 5). Larger effects are expected in plants with most of their biomass located near the sediment, such as American wildcelery.

The current sensitivity and environmental analyses give indications of the sensitivity of maximum plant biomass and end-of-year tuber number for variations in plant parameters and in environmental factors over a 1-year period. It is to be expected, however, that the small changes that occurred over this relatively short period will increase with time and that extrapolations in time will yield information on the likelihood for plant populations to ultimately persist or become extinct. Particularly, increased water turbidity, caused by increased phytoplankton or periphyton growth stimulated by eutrophication; increased erosion/ resuspension; and seasonal herbivory have been mentioned as decisive for the persistence of submersed plant populations.

7 Application Possibilities

POTAM can be used to assess behavior of a sago pondweed community under various site-specific and climatological conditions as demonstrated in Chapters 4, 5, and 6, and the simulation model can be run with user-specified input values for plant biomass, tuber size/tuber number concurrently initiated, and tuber bank density.

Effects of such man-made activities as mechanical harvesting at different times and at various water depths, and water level and water quality management can also be calculated using the model. Thus, in the latter case it can be used as a tool for aquatic plant and water management agencies (see for instance Bartell et al. 2000).

The current version of POTAM has been developed as a stand-alone simulation model. It can be relatively easily modified to communicate with ecosystem models because it is written in FORTRAN77 and its structure is simple. A similar growth model, developed for American wildcelery, has been used to calculate the potential production of plant biomass and tubers in Peoria Lake, IL, with modeled data on hydrodynamics as inputs, and plant parameter outputs spatially visualized through interfacing with a Geographical Information System (Black et al. in preparation). To facilitate use of the current model, a user's manual has been prepared (Best and Boyd, in preparation).

8 Discussion

The current model gives a reasonable description of the dynamics in plant biomass and tuber numbers of an established sago pondweed population under a variety of field conditions. As can be expected, the model is very sensitive to environmental changes affecting the light climate and, consequently, the carbon flow through the plant. The model is also sensitive to temperature, because the development phase of the plants is tied to degree-day (temperature) sum.

Light attenuation by periphyton may have large effects on submersed macrophytes with biomass usually remaining below the water surface (*Vallisneria Americana*) (Titus and Adams 1979) and those with most of their biomass concentrated just above the hydrosoil (*Ceratophyllum demersum*) (Best and Dassen 1987; Best and Jacobs 1990). Light extinction by periphyton has not yet been included in POTAM because no field data on periphyton biomass concomitant with photosynthetic activity were available. The recently (2002) collected data on periphyton mass and potential effects on the light climate within the macrophyte bed will be included in a later version.

Senescence, resulting in decreasing photosynthetic activity in aging plant parts, has been included in the model formulation, but because of lack of data this feature has not been activated. However, effects of senescence over the vertical plant axis proved to be negligible in other submersed plant species (Eurasian watermilfoil) (Best and Boyd 1999).

References

Aleem, A. A., and Samaan, A. A. (1969). "Productivity of Lake Mariut, Egypt. Part II. Primary production," *Internationale Revue der Hydrobiologie* 54, 491-527.

Amthor, J. S. (1984). "The role of maintenance respiration in plant growth," *Plant, Cell, and Environment* 7, 561-569.

Anderson, M. G., and Low, J. B. (1976). "Use of sago pondweed by waterfowl on Delta Marsh, Manitoba," *Journal of Wildlife Management* 40, 233-242.

Bartell, S. M., Campbell, K. R., Best, E. P. H., and Boyd, W. A. (2000). "Ecological risk assessment of the effects of the incremental increase of commercial navigation traffic (25, 50, 75, and 100 percent increase of 1992 baseline traffic) on submerged aquatic plants in the main channel and main channel borders," Upper Mississippi River – Illinois Waterway System Navigation Study, ENV Report 17, prepared by the Cadmus Group, Oak Ridge, TN, and the U.S. Army Engineer Research and Development Center, Vicksburg, MS, for the U.S. Army Engineer Districts, Rock Island, St. Louis, St. Paul.

Basiouny, F. M., Haller, W. T., and Garrard, L. A. (1978). "Survival of Hydrilla (Hydrilla verticillata) plants and propagules after removal from the aquatic habitat," *Weed Science* 26, 502-504.

Bellrose, F. C., Havera, S. P., Paveglio, F. L., and Steffeck, D. W. (1983). "Fate of the lakes in the Illinois River valley," *Illinois Natural History Survey Biology Note* 119.

Bergmeyer, H. U. (1970). "Methoden der Enzymatische Analyse." 2. Auflag. Verlag Chemie, Weinheim.

Best, E. P. H. (1981). "A preliminary model for growth of Ceratophyllum demersum L.," *Verhaendlungen des Internationales Vereinigung fuer Limnologie* 21, 1484-1491.

_____. (1982). "Hormonal interactions in *Ceratophyllum demersum*," *Aquatic Botany* 13, 87-95.

Best, E. P. H., and Boyd, W. A. (1996). "A simulation model for growth of the submersed aquatic macrophyte hydrilla (*Hydrilla verticillata* (L.F.) Royle." Technical Report A-96-8, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

_____. (1999). "A simulation model for growth of the submersed aquatic macrophyte Eurasian watermilfoil (*Myriophyllum spicatum* L.)," Technical Report E-99-3, U.S. Army Engineer Research and Development Center, Vicksburg, MS.

_____. (2001). "A simulation model for growth of the submersed aquatic macrophyte american wildcelery (*Vallisneria americana* Michx.)," Technical Report ERDC/EL TR-01-5, U.S. Army Engineer Research and Development Center, Vicksburg, MS.

_____. "POTAM (Version 1.0): A simulation model for growth of sago pondweed-User's guide" (in preparation) U.S. Army Engineer Research and Development Center, Vicksburg, MS.

Best, E. P. H., and Dassen, J. H. A. (1987). "Biomass, stand area, primary production characteristics and oxygen regime of the *Ceratophyllum demersum* L. population in Lake Vechten, The Netherlands," *Archiv fuer Hydrobiologie/Supplement* 76, 347-367.

Best, E. P. H., De Vries, D., and Reins, A. (1985). "The macrophytes in the Loosdrecht Lakes: A story of their decline in the course of eutrophication," *Verhaendlungen des Internationalen Vereinigungs Theoretische und Angewandte Limnologie* 22, 868-875.

Best, E. P. H., and Jacobs, F. H. H. (1990). "Potential and actual production of submerged aquatic angiosperms common in temperate regions." *Proceedings, 8th Symposium on Aquatic Weeds*, 39-47.

Best, E. P. H., and Visser, H. W. C. (1987). "Seasonal growth of the submerged macrophyte *Ceratophyllum demersum* L. in mesotrophic Lake Vechten in relation to insolation, temperature and reserve carbohydrates," *Hydrobiologia* 148, 231-243.

Bick, H., and Van Schaik, A. W. J. (1980). " Ecological vision border lakes." Advice of the Natural Science Committee of the Nature Conservation Council, 291 pp. (In Dutch).

Black, P., Best, E. P. H., Newcomb, E. A., Birkenstock, T., Boyt, B., Heath, R., and James, W. F. "A pilot study of *Vallisneria americana* changes related to hydraulic modifications to Peoria Lake" (in preparation), U.S. Army Engineer Research and Development Center, Hanover, NH.

Blanch, S. J., Ganf, G. G., Walker, K. F. (1998). "Growth and recruitment in *Vallisneria americana* as related to average irradiance in the water column," *Aquatic Botany* 61, 181-205.

Collins, C. D., and Wlosinski, J. H. (1985). "A macrophyte submodel for aquatic ecosystems," *Aquatic Botany* 33, 191-206.

Crow, G. E., and Hellquist, C. B. (2000). *Aquatic and wetland plants of North America.* 2, 36.

Dandy, J. E., and Taylor, G. (1946). "An account of *Potamogeton* x suecicus Richt. in Yorkshire and the Tweed," *Proceedings Botanical Society of Edinburgh* 34, 348-360.

Den Hartog, C. (1981). "Aquatic plant communities of poikilosaline waters," *Hydrobiologia* 81, 15-22.

Den Hartog, C. (1982). "Architecture of macrophyte-dominated aquatic communities." *Studies on aquatic vascular plants.* J.J. Symoens, S.S. Hoooper, and P. Compere, ed., Royal Botanical Society of Belgium, Brussels, 222-234.

De Vlaming, V., and Proctor, V. W. (1968). "Dispersal of aquatic organisms: Viability of seeds recovered from the droppings of captive killdeer and mallard ducks," *American Journal of Botany* 55, 20-26.

Dirksen, S. (1982). "The importance of pondweed for bewick swans in the Lauwersmeer," *Limosa* 55, 30-31 (In Dutch).

Doyle, R. D. (2000). "Effects of sediment resuspension and deposition on plant growth and reproduction," Upper Mississippi River – Illinois Waterway System Navigation Study, ENV Report 28, prepared by U.S. Army Engineer Research and Development Center, Vicksburg, MS, for U.S. Army Engineer Districts, Rock Island, St. Louis, St. Paul.

Fassett, N. C. (1957). "A manual of aquatic plants." University of Wisconsin Press, Madison, WI.

Fernald, M. L. (1950). *Gray's manual of botany.* 8th ed., American Book Company, New York, 1632 pp.

Fischer, J. R., and Claflin, T. O. (1992). "Macrophyte community changes in navigation Pool 8, Upper Mississippi River, between 1975 and 1991." *Proceedings Mississippi River Research Consortium, Inc.,* Vol. 24.

Giesen, W. B. J. T., Van Katwijk, M. M., and Den Hartog, C. (1990). "Eelgrass condition and turbidity in the Dutch Wadden Sea," *Aquatic Botany* 37, 71-85.

Gijzen, H. (1985). "Simulatie van drogestof-produktie en de Leaf Area Index van cassave." MS Thesis, Department of Tropical Crop Science, Wageningen Agricultural University, The Netherlands (In Dutch).

Gleason, H. A. (1968). The new Britton and Brown illustrated flora of the Northeastern United States and adjacent Canada. Hafner, New York, Vol 1, 482 pp.

Godfrey, R. K., and Wooten, J. W. (1997). *Aquatic and wetland plants of Southeastern United States, monocotyledons.* The University of Georgia Press, Athens, 711 pp.

Golterman, H. L. (1975). *Physiological limnology. An approach to the physiology of lake ecosystems.* Elsevier Scientific Publishing Company, Amsterdam, 489 pp.

Goudriaan, J. (1986). "A simple and fast numerical method for the computation of daily totals of crop photosynthesis," *Agricultural and Forest Meteorology* 38, 251-255.

Goudriaan, J., Van Keulen, H., and Van Laar, H. H. (1992). "Crop growth model for potential production (SUCROS1)." *Simulation of crop growth for potential and water-limited production situations (as applied to spring wheat).* Post-graduate course "Simulation of plant growth and crop production," Pontignano, Siena, Italy, 3-12 November, 1992, 1-25.

Green, W. E. (1960). "Ecological changes on the Upper Mississippi River Wildlife and Fish Refuge since inception of the 9-foot channel." *Proceedings 10th Annual Meeting Upper Mississippi Resources Conservation Committee,* 58-70.

Griffin, K. L. (1994). "Caloric estimates of construction cost and their use in ecological studies," *Functional Ecology* 8, 551-562.

Grime, J. P. (1979). "Plant strategies and vegetative processes." John Wiley & Sons, Chichester. 222 pp.

Guppy, H. B. (1897). "On the postponement of the germination of seeds of aquatic plants," *Proceedings of the Royal Physical Society of Edinburgh* 13, 344-360.

Gupta, R. K. (1968). *Flora Nainitalenses.* Mawagag Traders Publishing, New Delhi.

Haag, R. W. (1983). "Emergence of seedlings of aquatic macrophytes from lake sediments," *Canadian Journal of Botany* 61, 148-156.

Hagstrom, J. O. (1916). "Critical researches on the Potamogetons," *Kungl. Svenska Vet. Handl.* 55 (5), 281 pp.

Hammer, U. T., and Heseltine, J. M. (1988). "Aquatic macrophytes in saline lakes of the Canadian prairies," *Hydrobiologia* 158, 101-116.

Harrison, J. W. (1949). "*Potamogeton* in the Scottish Western isles, with some remarks on the general natural history of the species," *Transactions of the Botanical Society of Edinburgh* 35, 1-25.

Hettiararchi, P. L., and Triest, L. (1986). "Isoenzyme polymorphism of Potamogeton pectinatus L." *Proceedings of the 7th International Symposium on Aquatic Weeds.* European Weed Research Society and Association of Applied Biologists, 163-168.

Hewitt, B. R. (1958). "Spectrophotometric determination of total carbohydrate," *Nature* 182, 246-247.

Hodgson, R. H. (1966). "Growth and carbohydrate status of sago pondweed," *Weeds* 14, 263-268.

Hootsmans, M. J. M. (1991). "A growth analysis model for Potamogeton pectinatus L.." *Macrophytes, a key to understanding changes caused by eutrophication in shallow freshwater ecosystems.* M. J. M. Hootsmans and J. E. Vermaat, IHE Report Series 21, Delft, The Netherlands, 263-311.

Howard-Williams, C. (1978). "The growth and reproduction of aquatic macrophytes in a south temperate saline lake," *Verhaendlungen Internationale Vereinigung der Limnologie* 20, 1153-1158.

Howard-Williams, C. (1981). "Studies on the ability of a *Potamogeton pectinatus* community to remove dissolved nitrogen and phosphorus compounds from lake water," *Journal of Applied Ecology* 18, 619-637.

Hunt, R. (1982). *Plant growth curves.* Arnold, London.

Kadono, Y. (1982). "Distribution and habitat of Japanese *Potamogeton*," *Botanical Magazine of Tokyo* 95: 63-76.

Kalkman, L., and Van Wijk, R. J. (1984). "On the variation in chromosome number in *Potamogeton pectinatus* L.," *Aquatic Botany* 20, 343-349.

Kantrud, H. A. (1986). "Western Stump Lake, a major canvasback staging area in eastern North Dakota," *Prairie Naturalist* 18, 247-253.

Kantrud, H. A. (1990). "Sago pondweed (*Potamogeton pectinatus* L.): A literature review," Publication 176, U.S. Fish and Wildlife Service, Fish and Wildlife Resource, 89 pp.

Kartesz, J. T., and Kartesz, R. (1980). "A synonymized checklist of the vascular flora of the United States, Canada, and Greenland." Vol. II. *The biota of North America.* University of North Carolina Press, Chapel Hill, 498 pp.

Kautsky, L. (1987). "Life cycles of three populations of *Potamogeton pectinatus* at different degrees of wave exposure in the Asko area, Northern Baltic proper," *Aquatic Botany* 27, 177-186.

Klaine, S. J., and Ward, C. H. (1984). "Environmental and chemical control of vegetative dormant bud production in *Hydrilla verticillata*," *Annals of Botany* 53, 503-514.

Kooman, P. L. (1995). "Genotype-environment interaction in potato 2: Dry matter allocation and duration of the growth cycle." *Yielding ability of potato crops as influenced by temperature and daylength,* Ph. D. diss., Agricultural University Wageningen, Chapter 5, 71-89.

Korschgen, C. E. (1989). "Riverine and deepwater habitats for diving ducks." *Habitat management for migrating and wintering waterfowl in North America.* L. M. Smith, R. L. Pederson, and R. M. N. Kaminski, ed., Texas Tech University Press, Lubbock.

Korschgen, C. E., George, L. S., and Green, W. L. (1988). "Feeding ecology of canvasbacks staging on Pool 7 of the Upper Mississippi River." *Waterfowl in winter.* M.W. Weller, ed., University of Minnesota Press, Minneapolis, 237-250.

Lapirov, A. G., and Petukhova, L. V. (1985). "The rhythm of development of fennel-leaved pondweed in the Uglitch reservoir," *Biol vnutr. vod, Inform. Bull.* 66, 10-13 (In Russian).

Lohammar, G. (1938). "Wasserchemie und hohere Vegetation Schwedischer Seen," *Symb. Bot. Upsal.* 3, 1-252.

Lovvorn, J. R. (1989). "Distributional responses of canvasback ducks to weather and habitat change," *Journal of Applied Ecology* 26, 113-130.

Lovvorn, J. R., and Gillingham, M. P. (1996). "Food dispersion and foraging energetics: A mechanistic synthesis for field studies of avian benthivores," *Ecology* 77, 435-451.

Madsen, J. D., and Adams, M. S. (1988). "The seasonal biomass and productivity of the submerged macrophytes in a polluted Wisconsin stream," *Freshwater Biology* 20, 41-50.

Martin, A., Zim, H., and Nelson, A. (1951). *American wildlife and plants – A guide to wildlife food habits.* Dover Publications, Inc., New York, 500 pp.

Mason, H. L. (1969). *A flora of the marshes of California.* University of California Press, Berkeley, 878 pp.

Ng, E., and Loomis, R.S. (1984). "Simulation of growth and yield of the potato crop," Simulation Monographs, Pudoc, Wageningen, 147 p.

Ozimek, T., Prejs, K., and Prejs, A. (1986). "Biomass and growth rate of *Potamogeton pectinatus* L. in lakes of different trophic state," *Ekologia Polska* 34, 125-131.

Pederson, R. L., and Van der Valk, A. G. (1984). "Vegetation change and seed banks in marshes: Ecological and management implications," *Transactions of the North American Wildlife Natural Resources Conference* 49, 271-280.

Penning de Vries, F. W. T. (1975). "The cost of maintenance processes in plant cells," *Annals of Botany* 39, 77-92.

Penning de Vries, F. W. T., and Van Laar, H. H. (1982a). "Simulation of growth processes and the model BACROS." *Simulation of plant growth and crop production.* Pudoc, Wageningen, 99-102.

Penning de Vries, F. W. T., and Van Laar, H. H. (1982b). "Simulation of growth processes and the model BACROS." *Simulation of plant growth and crop production*. Pudoc, Wageningen, 114-131.

Penning de Vries, F. W. T., Jansen, D. M., Ten Berge, H. F. M., and Bakema, A. (1989a). "Morphological development and assimilate partitioning." *Simulation of ecophysiological processes of growth in several annual crops*. Chapter 3, Pudoc, Wageningen, 49-56.

Penning de Vries, F. W. T., Jansen, D. M., Ten Berge, H. F. M., and Bakema, A. (1989b). "Morphological development and assimilate partitioning." *Simulation of ecophysiological processes of growth in several annual crops*. Chapter 3, Pudoc, Wageningen, 73-115.

Philbrick, C. T., and Anderson, G. J. (1987). "Implications of pollen/ovule ratios and pollen size for the reproductive biology of *Potamogeton* and autogamy in aquatic angiosperms," *Systematic Botany* 12, 98-105.

Pilon, J. (1999). "Progress Report, 1998." Netherlands Institute of Ecology, Royal Dutch Academy of Sciences, Nieuwersluis, The Netherlands.

Pilon, J., and Santamaria, L. (2002). "Clonal variation in the thermal response of the submerged aquatic macrophyte *Potamogeton pectinatus*," *Journal of Ecology* 90, 141-152.

Pip, E. (1987). "The ecology of *Potamogeton* species in central North America," *Hydrobiologia* 153, 203-216.

Rabbinge, R., and De Wit, C. T. (1989). "Theory of modelling and systems management." *Simulation and systems management in crop protection*. R. Rabbinge, S. A. Ward and H. H. van Laar, ed., Chapter 1. Simulation Monographs 32, Pudoc, Wageningen, 1-12.

Ramirez, C., and San Martin, J. (1984). "Hydrophilous vegetation of a coastal lagoon in central Chile," *International Journal of Ecological and Environmental Sciences* 10, 93-110.

Ridley, H. N. (1930). *The dispersal of plants throughout the world*. L. Reeve and Company, Ltd., London, 744 pp.

Rogers, S. J. (1996). "Preliminary evaluation of submersed macrophyte changes in the Upper Mississippi River," *Lake and Reservoir Management* 10, 35-38.

Sahai, R., and Sinha, A. B. (1973). "Productivity of submerged macrophytes in polluted and non-polluted regions of the eutrophic Lake Ramgarh (U.P.)." *Aquatic weeds in South East Asia. Proceedings of a Regional Seminar on Noxious Aquatic Vegetation*, New Delhi, 12-17 December, 1973. C. K. Varshney and J. Rzoska, ed., 131-140.

Scheffer, M. (1991). "On the prediction of aquatic vegetation in shallow lakes," *Memorie dell' Istituto Italiano di Idrobiologia* 48, 207-217.

Scheffer, M., Bakema, A. H., and Wortelboer, F. G. (1993). "MEGAPLANT: A simulation model of the dynamics of submerged plants," *Aquatic Botany* 45, 341-356.

Sher-Kaul, S., Oertli, B., Castella, E., and Lachavanne, J. B. (1995). "Relationship between biomass and surface area of six submerged aquatic plant species," *Aquatic Botany* 51: 147-154.

Sinha, A. B. (1970). "Studies on the bioecology and production in Ramgarh Lake, Gorakhpur," Ph. D. diss., Gorakhpur University, India.

Spence, D. H. N., and Maberly, S. C. (1984). "Occurrence and ecological importance of HCO_3- use among aquatic higher plants." Inorganic carbon uptake by aquatic photosynthetic organisms. Proceedings of an International Workshop on Bicarbonate Use in Photosynthesis, University of California, Davis, August 18-22, 1984, W. J. Lucas and J. A. Berry, ed., 125-145.

Spencer, D. F. (1987). "Tuber size and planting depth influence growth of *Potamogeton pectinatus* L.," *The American Midland Naturalist* 118, 77-84.

Spencer, D. F., and Anderson, L. W. J. (1986). "Photoperiod responses in monoecious and dioecious *Hydrilla verticillata*," *Weed Science* 34, 551-557.

Spencer, D. F., and Anderson, L. W. J. (1987). "Influence of photoperiod on growth, pigment composition and vegetative propagule formation for *Potamogeton nodosus* Poir. and *Potamogeton pectinatus* L.," *Aquatic Botany* 28, 102-112.

Spencer, W., and Bowes, G. (1990). "Ecophysiology of the world's most troublesome aquatic weeds." *Aquatic Weeds, The ecology and management of nuisance aquatic vegetation.* A. H. Pieterse and K. J. Murphy, ed., Oxford University Press, 39-74.

Spencer, D. F., Ksander, G. G., and Whitehand, L. C. (1994). "Estimating the abundance of subterranean propagules of submersed aquatic plants," *Freshwater Biology* 31, 191-200.

Spencer, D. F., Ryan, F. J., and Ksander, G. G. (1997). "Construction costs for some aquatic plants," *Aquatic Botany* 56, 203-214.

Spink, A., and Rogers, S. (1996). "The effects of a record flood on the aquatic vegetation of the Upper Mississippi River System: Some preliminary findings," *Hydrobiologia* 340, 51-57.

Spitters, C. J. T. (1986). "Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis. II. Calculation of canopy photosynthesis," *Agricultural and Forest Meteorology* 38, 231-242.

Sterling, M. R. (1970). "Seasonal utilization of sago pondweed by waterfowl at Bear River Migratory Bird Refuge, Utah," M.S. Thesis, Utah State University, Logan. 121 pp.

Sutton, D. L., Littell, R. C., and Langeland, K. A. (1980). "Intraspecific competition of *Hydrilla verticillata*," *Weed Science* 28, 425-428.

Terras, J. A. (1900). "Notes on the germination of winter-buds of Hydrocharis morsus-ranae," Transactions, Proceedings of the Botanical Society of Edinburgh 21, 318-329.

Thornley, J. H. M., and Johnson, I. R. (1990a). "Temperature effects on plant and crop processes." *Plant and crop modeling, A mathematical approach to plant and crop physiology*. Clarendon Press, Oxford, 139-144.

Thornley, J. H. M., and Johnson, I. R. (1990b). "Plant growth functions." *Plant and crop modeling, A mathematical approach to plant and crop physiology*. Clarendon Press, Oxford, 74-89.

Titus, J., and Adams, M. A. (1979). "Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx," *Oecologia* 40, 273-286.

Titus, J., Goldstein, R. A., Adams, M. A., Mankin, J. B., O'Neill, R. V., Weiler, P. R., Shugart, H. H., and Booth, R. S. (1975). "A production model for *Myriophyllum spicatum* L.," *Ecology* 56, 1129-1138.

Uhl, N. W. (1947). "Studies in the floral morphology and anatomy of certain members of the Helobiae," Ph.D Thesis, Cornell University, USA.

U.S. Department of Agriculture. (1982). "National list of scientific plant names. Vol.1. List of plant names," SCS-TP-159, U.S. Department of Agriculture, Soil Conservation Service.

Van, T. K., Haller, W. T., and Bowes, G. (1978). "Some aspects of the competitive biology of Hydrilla." *Proceedings, 5th EWRS International Symposium on Aquatic Weeds*, Amsterdam (The Netherlands). 117-126.

Van der Bijl, L., Sand-Jensen, K., and Hjermind, A. L. (1989). "Photosynthesis and canopy structure of a submerged plant *Potamogeton pectinatus*, in a Danish lowland stream," *Journal of Ecology* 77, 947-962.

Van Dijk, G. M., and Achterberg, E. P. (1992). "Light climate in the water column of a shallow eutrophic lake (Lake Veluwe) in The Netherlands," *Archiv fuer Hydrobiologie* 125, 257-278.

Van Dijk, G. M., Breukelaar, A. W., and Gijlstra, R. (1992). "Impact of light climate history on seasonal dynamics of a field population of *Potamogeton pectinatus* L. during a three year period (1986-1988)," *Aquatic Botany* 43, 17-41.

Van Keulen, H. (1976). "Evaluation of models," *Critical evaluation of systems analysis in ecosystems research and management*, G. W. Arnold and C. T. de Wit, ed., Simulation Monographs, Pudoc, Wageningen, 22-29.

Van Kraalingen, D. W. G. (1995). "The FSE System for Crop Simulation." *AB-DLO Report*. Wageningen, The Netherlands. 53 pp.

Van Vierssen, W., and Verhoeven, J. T. A. (1983). "Plant and animal communities in brackish supra-littoral pools ("dobben") in the northern part of The Netherlands," *Hydrobiologia* 98, 203-221.

Van Wijk, R. J. (1983). "Life-cycles and reproductive strategies of *Potamogeton pectinatus* L. in The Netherlands and the Camargue (France)," *Proceedings of the International Symposium on Aquatic Macrophytes,* Nijmegen, The Netherlands, 18-23 September, 1983. 317-321.

Van Wijk, R. J. (1986). "Life cycle characteristics of *Potamogeton pectinatus* L. in relation to control." *Proceedings EWRS/AAA 7th Symposium on Aquatic Weeds.* 375-379.

Van Wijk, R. J. (1988)."Ecological studies on *Potamogeton pectinatus* L. I. General characteristics, biomass production and life cycles under field conditions," *Aquatic Botany* 31, 211-258.

Van Wijk, R. J. (1989)."Ecological studies on *Potamogeton pectinatus* L. III. Reproductive strategies and germination ecology," *Aquatic Botany* 33, 271-299.

Van Wijk, R. J., Van Goor, E., and Verkley, J. A. C. (1988). "Ecological studies on *Potamogeton pectinatus* L. II. Autecological characteristics with emphasis on salt tolerance, intraspecific variation and isoenzyme patterns," *Aquatic Botany* 32, 239-260.

Vermaat, J. E., and Hootsmans, M. J. M. (1994a). "Intraspecific variation in *Potamogeton pectinatus* L.: A controlled laboratory experiment." *Lake Veluwe, a macrophyte-dominated system under eutrophication stress.* W. Van Vierssen, M. Hootsmans, and J. Vermaat, ed., Kluwer Academic Publishers, Dordrecht, Boston, London, Chapter 4, 26-39.

Vermaat, J. E., and Hootsmans, M. J. M. (1994b). "Light-response curves of *Potamogeton pectinatus* L. in a temperature-light gradient." *Lake Veluwe, a macrophyte-dominated system under eutrophication stress,* W. Van Vierssen, M. Hootsmans, and J. Vermaat, ed., Kluwer Academic Publishers, Dordrecht, Boston, London, Chapter 6, 62-117.

Voss, E. (1972). *Michigan Flora. Part I — Gymnosperms and monocots.* Cranbrook Institute of Science, Bloomfield Hills, Michigan. 488 pp.

Weber, J. A., and Nooden, L. D. (1974). "Turion formation and germination in *Myriophyllum verticillatum*: Phenology and its interpretation," *Michigan Botanist* 13, 151-158.

Westlake, D. F. (1964). "Light extinction, standing crop and photosynthesis within weed beds," *Verhaendlungen internationaler Vereinigung der Limnologie* 15, 415-425.

Wetzel, R. L., and Neckles, H. A. (1996). "A model of *Zostera marina* L. photosynthesis and growth: Simulated effects of selected physical-chemical variables and biological interactions," *Aquatic Botany* 26, 307-323.

Wiegleb, G. (1978). "Untersuchungen uber den Zusammenhang zwischen hydrochemischen Umweltfaktoren und Makrophytenvegetation in stehenden Gewassern," *Archiv fuer Hydrobiologie* 83, 443-484.

Williams, K., Percival, F., Merino, J., and Mooney, H. A. (1987). "Estimation of tissue construction cost from heat combustion and organic nitrogen content," *Plant Cell and Environment* 10, 725-734.

Winston, R. E., and Gorham, P. R. (1979). "Turions and dormancy states in *Utricularia vulgaris*," *Canadian Journal of Botany* 57, 2740-2749.

Wong, S. L., and Clark, B. (1976). "Field determination of the critical nutrient concentration for *Cladophora* in streams," *Journal of the Fisheries Research Board of Canada* 33, 85-92.

Yeo, R. R. (1965). "Life history of sago pondweed," *Weeds* 13, 314-321.

Appendix A
Model Listing

```
*--------------------------------------------------------------------------------*
* SUBROUTINE MODEL                                                               *
* Authors: Elly Best & Will Boyd                                                 *
* Date   : 18 August 1999                                                        *
* Purpose: This subroutine is the translated FST file                           *
*                                                                               *
* FORMAL PARAMETERS:  (I=input,O=output,C=control,IN=init,T=time)               *
* name          type    meaning                                  units   class*
* ------        ------  -----------                              ------  ------*
* DELT          R4      Time step of integration                 d        I   *
* DOY           R4      Day number within year of simulation (REAL)  D    I   *
* FILEIN        C*      Name of file with input model data        -        I   *
* FINTIM        R4      Finish time of simulation (=day number)   d        I   *
* IDOY          I4      Day number within year of simulation (INTEGER)  d  I   *
* ITASK         I4      Task that subroutine should perform       -        I   *
* IUNITD        I4      Unit of input file with model data        -        I   *
* IUNITO        I4      Unit of output file                       -        I   *
* IUNITL        I4      Unit number for log file messages         -        I   *
* IYEAR         I4      Year of simulation (INTEGER)              y        I   *
* LAT           R4      Latitude of site                         dec.degr. I  *
* LONG          R4      Longitude of site                        dec.degr. I  *
* ELEV          R4      Elevation of site                        M        I   *
* OUTPUT        L4      Flag to indicate if output should be done -        I   *
* RAIN          R4      Daily amount of rainfall                  mm.d-1   I   *
* RDD           R4      Daily shortwave radiation                J.m-2.d-1 I  *
* STTIME        R4      Start time of simulation (=day number)    d        I   *
* TERMNL        L4      Flag to indicate if simulation is to stop -        I/O *
* TMMN          R4      Daily minimum temperature                degrees C I  *
* TMMX          R4      Daily maximum temperature                degrees C I  *
* VP            R4      Early morning vapour pressure             kPa      I   *
* WN            R4      Daily average windspeed                   m/s      I   *
* WSTAT         C6      Status code from weather system           -        I   *
* WTRTER        L4      Flag whether weather can be used by model -        O   *
* YEAR          R4      Year of simulation (REAL)                 y        I   *
*                                                                               *
* Fatal error checks: if one of the characters of WSTAT = '4', indicates missing weather  *
* Warnings      : none                                                          *
* Subprograms called: models as specified by the user                          *
* File usage    : IUNITD,IUNITD+1,IUNITO,IUNITO+1,IUNITL                        *
*--------------------------------------------------------------------------------*
```

```
      SUBROUTINE MODEL (ITASK , IUNITD, IUNITO, IUNITL,
     &           FILEIN,
     &           OUTPUT, TERMNL,
     &           DOY  , IDOY , YEAR , IYEAR,
     &           TIME , STTIME, FINTIM, DELT ,
     &           LAT  , LONG , ELEV , WSTAT , WTRTER,
     &           RDD  , TMMN , TMMX , VP  , WN, RAIN)

*-----Title of the program
*    <Fill in your title here>
*    Potam1

IMPLICIT REAL (A-Z)

*-----Formal parameters

      INTEGER  ITASK , IUNITD, IUNITO, IUNITL, IDOY, IYEAR
      LOGICAL  OUTPUT, TERMNL, WTRTER
      CHARACTER*(*) FILEIN, WSTAT
      REAL DOY, YEAR, TIME, STTIME, FINTIM, DELT
      REAL LAT, RDD, TMMN, TMMX, VP, WN, RAIN
      REAL TMAX(365), TMIN(365)

*-----Standard local declarations
      INTEGER IWVAR,ITOLD,IDAY,DDELAY,SSURPR
      CHARACTER WUSED*6

*-----State variables, initial values and rates
      REAL DVS   , NUL   , DVR
      REAL TREMOB, IREMOB,TMPSUM
      REAL TWLVD , IWLVD , DLV
      REAL TWLVG , IWLVG , NGLV
      REAL TWSTD , IWSTD , DST
      REAL TWSTG , IWSTG , NGST
      REAL TWRTD , IWRTD , DRT
      REAL TWRTG , IWRTG , NGRT
      REAL TMP2  , INTUB

*-----Model parameters
      REAL AMX   , CVT   , DAYEM , DELAY ,REDAM
      REAL NPL   , CRIFAC, SURPER
      REAL RC    , TBASE
      REAL ROC   , TL    , RCSHST, EE    , RDTU
      REAL NNTUB , NGTUB , NTUBD , NDTUB , RTR
      REAL TWGTUB, TWNTUB, NTUBPD, NINTUB, TWCTUB
      REAL HAR   , HARDAY, HARDEP

*-----Auxiliary variables
      REAL AMAX    , AMTMP , ASRQ  , COSLD , WTMP
      REAL DAVTMP, DAY    , DAYL  , YRNUM , WST
      REAL DDTMP , DS0    , DSINB , DSINBE
      REAL DTEFF , DTGA   , FGROS, FLV    , FRT
      REAL FST    , GLV    , GPHOT, GRT    , GST
      REAL GTW    , MAINT  , MAINTS, NTM   , PI
      REAL RDR    , RDS    , REMOB, SC     , SUM
      REAL TGWM   , SINLD  , TGW   , TEFF  , TRANS
      REAL TW     , WLV    , WRT    , SURFAC
```

```
*-----AFGEN functions
*     REAL AMDVST
*     INTEGER IMAMDV, ILAMDV
*     PARAMETER (IMAMDV = 40)
*     DIMENSION AMDVST(IMAMDV)
      REAL AMTMPT
      INTEGER IMAMTM, ILAMTM
      PARAMETER (IMAMTM =  40)
      DIMENSION AMTMPT(IMAMTM)
      REAL DPTT
      INTEGER IMDPT, ILDPT
      PARAMETER (IMDPT = 730)
      DIMENSION DPTT (IMDPT)
      REAL FLT
      INTEGER IMFLT, ILFLT
      PARAMETER (IMFLT  =  40)
      DIMENSION FLT (IMFLT)
      REAL FLVT
      INTEGER IMFLVT, ILFLVT
      PARAMETER (IMFLVT =  40)
      DIMENSION FLVT (IMFLVT)
      REAL FRTT
      INTEGER IMFRTT, ILFRTT
      PARAMETER (IMFRTT =  40)
      DIMENSION FRTT (IMFRTT)
      REAL FSTT
      INTEGER IMFSTT, ILFSTT
      PARAMETER (IMFSTT =  40)
      DIMENSION FSTT (IMFSTT)
      REAL LT, KT
      INTEGER IMN1,ILT,IKT
      PARAMETER (IMN1  = 730)
      DIMENSION LT(IMN1), KT(IMN1)
      REAL NTMT, TGWMT
      INTEGER IMMEAS, ILMEAS
      PARAMETER (IMMEAS =  40)
      DIMENSION NTMT(IMMEAS), TGWMT(IMMEAS)
      REAL RDRT
      INTEGER IMRDRT, ILRDRT
      PARAMETER (IMRDRT =  40)
      DIMENSION RDRT  (IMRDRT)
      REAL RDST
      INTEGER IMRDST, ILRDST
      PARAMETER (IMRDST =  40)
      DIMENSION RDST  (IMRDST)
      REAL TEFFT
      INTEGER IMTEFF, ILTEFF
      PARAMETER (IMTEFF =  40)
      DIMENSION TEFFT(IMTEFF)
      REAL WTMPT
      INTEGER IMWTMP, ILWTMP
      PARAMETER (IMWTMP = 730)
      DIMENSION WTMPT (IMWTMP)
```

```
*-----Used functions
      REAL LINT , INSW
      SAVE

      DATA ITOLD /4/
*-----Code for the use of RDD, TMMN, TMMX, VP, WN, RAIN  (in that order)
*     A letter 'U' indicates that the variable is used in calculations
      DATA WUSED/'UUU---'/

*-----Check weather data availability
      IF (ITASK.EQ.1.OR.ITASK.EQ.2.OR.ITASK.EQ.4) THEN
          DO 10 IWVAR=1,6
*-----Is there an error in the IWVAR-th weather variable ?
          IF (WUSED(IWVAR:IWVAR).EQ.'U' .AND.
     &        WSTAT(IWVAR:IWVAR).EQ.'4') THEN
                 WTRTER = .TRUE.
                 TERMNL = .TRUE.
                 ITOLD  = ITASK
                 RETURN
          END IF
10    CONTINUE
      END IF

      IF (ITASK.EQ.1) THEN
*                                                         *
*              INITIALIZATION  SECTION                    *
*              ===============================            *
*-----Send title to output file                           *

*-----Open input file
          CALL RDINIT (IUNITD, IUNITL, FILEIN)

*-----Read 1st value in MODEL.DAT file ... year number
          CALL RDSREA ('YRNUM ',YRNUM )

*-----Read initial states
          CALL RDSREA ('INTUB ',INTUB )
          CALL RDSREA ('IREMOB',IREMOB)
          CALL RDSREA ('IWLVD ',IWLVD )
          CALL RDSREA ('IWLVG ',IWLVG )
          CALL RDSREA ('IWRTD ',IWRTD )
          CALL RDSREA ('IWRTG ',IWRTG )
          CALL RDSREA ('IWSTD ',IWSTD )
          CALL RDSREA ('IWSTG ',IWSTG )
          CALL RDSREA ('NUL    ',NUL   )
          CALL RDSREA ('REMOB ',REMOB )

*-----Read model parameters
          CALL RDSREA ('AMX       ',AMX   )
          CALL RDSREA ('CRIFAC  ',CRIFAC)
          CALL RDSREA ('CVT      ',CVT  )
          CALL RDSREA ('DAYEM ',DAYEM )
          CALL RDSREA ('DELAY   ',DELAY )
          CALL RDSREA ('EE        ',EE   )
          CALL RDSREA ('HAR      ',HAR  )
          CALL RDSREA ('HARDAY',HARDAY)
          CALL RDSREA ('HARDEP',HARDEP)
          CALL RDSREA ('NDTUB ',NDTUB )
```

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```
      CALL RDSREA ('NINTUB ',NINTUB)
      CALL RDSREA ('NPL     ',NPL  )
      CALL RDSREA ('RC      ',RC   )
      CALL RDSREA ('RCSHST',RCSHST)
      CALL RDSREA ('RDTU   ',RDTU )
      CALL RDSREA ('REDAM ',REDAM )
      CALL RDSREA ('ROC    ',ROC  )
      CALL RDSREA ('RTR    ',RTR  )
      CALL RDSREA ('SURPER',SURPER)
      CALL RDSREA ('TBASE ',TBASE )
      CALL RDSREA ('TL      ',TL   )
      CALL RDSREA ('TWCTUB',TWCTUB)

*-----Read AFGEN functions
      CALL RDAREA ('AMTMPT',AMTMPT,IMAMTM,ILAMTM)
      CALL RDAREA ('DPTT   ',DPTT ,IMDPT ,ILDPT )
      CALL RDAREA ('FLT     ',FLT  ,IMFLT , ILFLT)
      CALL RDAREA ('FLVT   ',FLVT ,IMFLVT,ILFLVT)
      CALL RDAREA ('FSTT    ',FSTT ,IMFSTT,ILFSTT)
      CALL RDAREA ('FRTT    ',FRTT ,IMFRTT,ILFRTT)
      CALL RDAREA ('KT      ',KT   ,IMN1 ,IKT  )
      CALL RDAREA ('LT      ',LT   ,IMN1 ,ILT  )
      CALL RDAREA ('NTMT    ',NTMT ,IMMEAS,ILMEAS)
      CALL RDAREA ('RDRT    ',RDRT ,IMRDRT,ILRDRT)
      CALL RDAREA ('RDST    ',RDST ,IMRDST,ILRDST)
      CALL RDAREA ('TEFFT  ',TEFFT ,IMTEFF,ILTEFF)
      CALL RDAREA ('TGWMT ',TGWMT ,IMMEAS,ILMEAS)
      CALL RDAREA ('WTMPT ',WTMPT ,IMWTMP,ILWTMP)

***            INITIAL CALCULATIONS        ***
*              ======================        *


*-----Initially known variables to output
*     Send title(s) to OUTCOM

*-----Initialize state variables
*     Start at the beginning of the developmental cycle
      DVS   = NUL
      TMPSUM = NUL

*-----Initialize counter KCOUNT & SURFACE
      KCOUNT = 0
      SURFAC = 0

*-----DELAY  and SSURPR variables are set from a REAL to an INTEGER
      DDELAY = DELAY
      SSURPR = SURPER

*-----Initialize weights of plant organs
      IF (YRNUM .EQ. 1.)THEN
      TWLVD  = IWLVD
      TWLVG  = IWLVG
      TWSTD  = IWSTD
      TWSTG  = IWSTG
      TWRTD  = IWRTD
      TWRTG  = IWRTG
      ENDIF
```

```
*-----Initialize remobilization
      TREMOB = IREMOB


*-----Initialize tuber numbers and weight
          NNTUB  = 0.0
      IF (NDTUB .LT. 30.)NPL = NDTUB
          NGTUB   = NPL
      IF(YRNUM.EQ.1.)NTUBD  = RDTU * NDTUB * TEFF
      NDTUB  = NDTUB - (NTUBD-NTUBPD)
          TWGTUB  = NPL * INTUB
          TWNTUB  = 0.0

      ELSE IF (ITASK.EQ.2) THEN

***               RATES OF CHANGE            ***
*                 =================            *


*-----Weights of plant organs
          WLV   = TWLVG + TWLVD
          WST   = TWSTG + TWSTD
          WRT   = TWRTG + TWRTD
          TGW   = TWLVG + TWSTG + TWRTG


*-----Total live weight never >1952 g DW / m2 ; cf. Howard Williams, 1978.
      TGW   = AMIN1 (TGW, 1952.)

****              RATE CALCULATIONS            ***
*                 ==================             *


*-----Julian day number
          DAY = 1.+MOD (TIME-1.,365.)


*-----If water temperatures are available, temperature dependent processes are related to
*         water temperature; otherwise they are related to air temperature with a lag period in
*         day(s) to be chosen by substituting number given for DELAY in MODEL.DAT

          WTMP = LINT (WTMPT,ILWTMP,DAY)
          DPT  = LINT (DPTT ,ILDPT, DAY)
          IDAY = DAY

          TMAX(IDAY) = TMMX
          TMIN(IDAY) = TMMN
      IF (DAY .LE. DDELAY) THEN
          DAVTMP = 0.5 * (TMAX(1)+TMIN(1))
        DDTMP  = AMAX1(TMAX(1) - 0.25 * (TMAX(1)-TMIN(1)),5.)
      ELSE
        DAVTMP = 0.5 * (TMAX(IDAY-DDELAY)+TMIN(IDAY-DDELAY))
        DDTMP  = AMAX1(TMAX(IDAY-DDELAY) - 0.25 *
      &        (TMAX(IDAY-DDELAY)-TMIN(IDAY-DDELAY)),5.)
      ENDIF

      IF (DAVTMP .LT. 5.0)DAVTMP = 5.0

          IF (WTMP .GT. 0.0) THEN
          DAVTMP = WTMP
          DDTMP  = WTMP
          ENDIF
```

```
*-----Effective temperature influencing remobilization and translocation processes

    TEFF = LINT(TEFFT,ILTEFF,DDTMP)

*-----Relative tuber growth rate
        RTRL   = RTR * TEFF

*-----Measured tuber numbers and measured total live plant dry weight
        NTM  = LINT (NTMT,ILMEAS,DAY)
        TGWM = LINT (TGWMT,ILMEAS,DAY)

*-----SBRT ASTRO call to introduce day length into MAIN
    CALL ASTRO
    $ (DAY,LAT,SC,DS0,SINLD,COSLD,DAYL,DSINB,DSINBE)

*------Tuber behavior.
*     Sprouting of tubers leads to carbohydrate remobilization to form
*          new plants, is related to DVS (calibrated to proper day length and temperature)
*          provided tubers are present; sprouting can only take place before normal anthesis
*          time (DVS=1). If plants lose their biomass after DVS = 1, no new tubers
*          sprout that same year. Tubers do sprout the next year, provided that tubers
*          are present. Tubers are depleted up to 10 percent of their DW (per tuber).

    TWTUB = NDTUB * INTUB
    TWTUBD = NTUBD * INTUB

    IF (TWTUB .LE. 0.0)TWTUB = 0.

    IF (TWTUB .EQ. 0 .AND. DAY .EQ. 1)THEN
    WRITE(*,*)' There are no tubers !! -- Press <ENTER> '
    READ(*,*)
    STOP
    ENDIF

*     Initialize variable(s) used in condition statement
*     Tropical ... Latitude is less than or equal to 33 deg
    IF (LAT .LE. 33.)THEN
    VAR1 = .336
    VAR2 = 1.6
    ELSE
*     Temperate ... Latitude is greater than 33 deg
    VAR1 = .210
    VAR2 = 1.0
    ENDIF

    IF (DVS .GE. VAR1 .AND. DVS .LT. VAR2)THEN
cPOTAMIN      IF (DVS .GE. .210 .AND. DVS .LT. 1.) THEN
cPOTAMIN      IF (DVS .GE. .336 .AND. DVS .LT. 1.6) THEN
        TWGTUB = INTGRL (TWGTUB,- REMOB,DELT)
        TWGTUB = AMAX1(0.0,TWGTUB)
     IF (NDTUB .GT. 0.) THEN
       REMOB  = TWGTUB * ROC * TEFF
     ENDIF
      IF (TWGTUB .LE. (0.01 * NPL * INTUB)) NGTUB = 0.0
    ELSE
        REMOB = 0.0
```

```
      ENDIF

*-----New tuber formation takes place at DVS >1 (temperate), daylength< 16 h, and 5 <water
*          temperature< 28 oC, provided plant wght > 0.1 g DW m-2; it continues until the
*          weight of that tuber class reaches the critical tuber weight equal to (number of
*          plants m-2)x(tuber number per plant)x tuber weight per tuber).

         IF (REMOB .EQ. 0.0) THEN

*     Initialize variable(s) used in condition statement
*     Tropical ... Latitude is less than or equal to 33 deg
         IF (LAT .LE. 33.)THEN
         VAR1 = 1.6
         ELSE
*     Temperate ... Latitude is greater than 33 deg
         VAR1 = 1.0
         ENDIF

         IF (DVS .GT. VAR1 .AND. DAYL .LT. 16.)THEN
cPOTAMIN         IF (DVS.GT.1.0 .AND. DAYL.LT.16.)THEN
cPOTAMIN         IF (DVS.GT.1.6 .AND. DAYL.LT.16.)THEN
         IF (DDTMP .GT. 5.0 .AND. DDTMP .LT. 28.0)THEN
         IF (TGW. GT. 0.1) THEN

            NNTUB = NPL * NINTUB
            TRANS = AMAX1 (0.,(RTRL * (1./CVT) * (GPHOT-MAINT)))

            TWNTUB = INTGRL (TWNTUB, TRANS, DELT)
            ELSE
            TWNTUB = 0.0
            ENDIF

            IF (TWNTUB .GE. TWCTUB) THEN
*-----When the new tuber class is finished, the new tubers are added to the total number of
*       dormant tubers
               NDTUB = NDTUB + (NPL * NINTUB)
               NTUBD = RDTU * NDTUB * TEFF

*-----Reset new tuber number and weight back to zero
               NNTUB  = 0.0
               TWNTUB = 0.0
               ENDIF
            ELSE
            TRANS = 0.0
            ENDIF
         ELSE
         TRANS = 0.0
         ENDIF
         ELSE
         TRANS = 0.0
         ENDIF

*-----Recalculate tuber numbers daily
         IF (DAY .GT. 1.0) THEN

*-----NNTUB not added because they were included in NDTUB when reaching the total
```

```
*        critical dry weight of new tubers TWCTUB
         ENDIF

*-----Dry matter and its partitioning over the plant organs
         TW   = TGW + (TWLVD + TWSTD + TWRTD)

         FLV = LINT(FLVT ,ILFLVT,DVS)
         FST = LINT(FSTT ,ILFSTT,DVS)
         FRT = LINT(FRTT ,ILFRTT,DVS)
         FL  = LINT(FLT  ,ILFLT ,DVS)

*-----Growth of plant organs, maintenance respiration and translocation
        ASRQ = 1.46*FLV+1.51*FST+1.44*FRT
        MAINTS = 0.016*TWLVG+0.01*TWSTG+0.015*TWRTG
         MAINT  = MAINTS * TEFF

*-----Sprouting tubers die if the resulting plant biomass has a negative net photosynthesis
*          during a user-defined number of consecutive days (27 is nominal). If this event
*          occurs, the program stops, and writes 'SURFAC'; By pressing enter, the program
*          continues
*      ... KCOUNT is a counter variable, which counts the days with negative net photosynthesis

      IF (GPHOT .LT. MAINT) THEN
       KCOUNT = KCOUNT + 1
      ELSE
       KCOUNT = 0
      ENDIF

      IF (KCOUNT.EQ.SSURPR .AND. SURFAC.LT.1.) THEN
        write(*,*)' KCOUNT = ',KCOUNT,'  SURFAC = ',SURFAC
        read(*,*)
        TWLVD = TWLVD + TWLVG
        TWSTD = TWSTD + TWSTG
        TWRTD = TWRTD + TWRTG

        TWLVG = 0.0
        TWSTG = 0.0
        TWRTG = 0.0
        REMOB = 0.0
        NDTUB = AMAX1 (0., NDTUB-NPL)

*    Initialize variable(s) used in condition statement
*    Tropical ... Latitude is less than or equal to 33 deg
      IF (LAT .LE. 33.)THEN
      VAR1 = 1.6
      ELSE
*    Temperate ... Latitude is greater than 33 deg
      VAR1 = 1.0
      ENDIF
*
      IF (DVS .LT. VAR1 .AND. NDTUB .GT. 0.) NGTUB = NPL
cPOTAMIN        IF (DVS .LT. 1.0 .AND. NDTUB .GT. 0.) NGTUB = NPL
cPOTAMIN        IF (DVS .LT. 1.6 .AND. NDTUB .GT. 0.) NGTUB = NPL
      ENDIF

*    Initialize variable(s) used in condition statement
```

```
*     Tropical ... Latitude is less than or equal to 33 deg
      IF (LAT .LE. 33.)THEN
      VAR1 = 3.2
      ELSE
*     Temperate ... Latitude is greater than 33 deg
      VAR1 = 2.001
      ENDIF
*
*-----Relative death rates
      RDR  = INSW (DVS-VAR1,0.,LINT (RDRT,ILRDRT,DAVTMP))
      RDS  = INSW (DVS-VAR1,0.,LINT (RDST,ILRDST,DAVTMP))
cPOTAMIN       RDR  = INSW (DVS-2.001,0.,LINT (RDRT,ILRDRT,DAVTMP))
cPOTAMIN       RDS  = INSW (DVS-2.001,0.,LINT (RDST,ILRDST,DAVTMP))
cPOTAMIN       RDR  = INSW (DVS-3.2,0.,LINT (RDRT,ILRDRT,DAVTMP))
cPOTAMIN       RDS  = INSW (DVS-3.2,0.,LINT (RDST,ILRDST,DAVTMP))


*-----Development rates
*
*     Initialize variable(s) used in condition statement
*     Tropical ... Latitude is less than or equal to 33 deg
      IF (LAT .LE. 33.)THEN
      VAR1 =1.6
      VAR2 = 20.0
      ELSE
*     Temperate ... Latitude is greater than 33 deg
      VAR1 = 1.0
      VAR2 = 20.0
      ENDIF
*
      IF(DAVTMP .LT. 3.0) THEN
        DVR = 0.0
      ELSE IF (DVS .LE. VAR1) THEN
cPOTAMIN      ELSE IF (DVS.LE.1.) THEN
cPOTAMIN      ELSE IF (DVS.LE.1.6) THEN
        DVR = 0.015*DAVTMP/30
      ELSE IF (DVS .GT. VAR1 .AND. DVS .LT. VAR2) THEN
cPOTAMIN      ELSE IF (DVS.GT.1. .AND. DVS .LT. 20.0) THEN
cPOTAMIN      ELSE IF (DVS.GT.1.6 .AND. DVS .LT. 20.0) THEN
        DVR = 0.040*DAVTMP/30
      ENDIF

*-----Calculation of astronomic day length
      CALL ASTRO
      $ (DAY,LAT,SC,DS0,SINLD,COSLD,DAYL,DSINB,DSINBE)

*-----Daily temperature after 1.January, with base temperature
*     specified by user (given in MODEL.DAT)
          DTEFF = AMAX1(0.,DAVTMP-TBASE)

*-----Calculation quantities dead plant material
          DLV  = TWLVG * RDR
          DST  = TWSTG * RDR
          DRT  = TWRTG * RDR

*-----Shoot photosynthesis at light saturation and daytime temperature effect on shoot photosynthesis
          AMAX  = AMAX1(0.00001,AMX * AMTMP)
```

```
            AMAX   = AMAX * REDAM
            AMTMP = LINT(AMTMPT,ILAMTM,DDTMP)


*-----Before calling TOTASS, determine light extinction coefficients of plants (K) and of water (L)
      L = LINT(LT,ILT,TIME)
      K = LINT(KT,IKT,DVS)


*-----Daily total gross assimilation

          CALL TOTASS
     $   (SC,DAYL,SINLD,COSLD,DSINBE,RDD,RC,L,K,AMAX,EE,
     $    TL,DPT,RCSHST,TGW,FGROS,FL,FLV,FRT,FST,WLV,WST,
     $    DAY,HAR,HARDAY,HARDEP,DTGA,NPL,IRS,REMOB,TWLVG,
     $    TWSTG,TWRTG,SURFAC,CRIFAC)


*------If DVS is greater than one then REMOB should be set to zero


*      Initialize variable(s) used in condition statement
*      Tropical ... Latitude is less than or equal to 33 deg
       IF (LAT .LE. 33.)THEN
       VAR1 = 1.6
       ELSE
*      Temporate ... Latitude is greater than 33 deg
       VAR1 = 1.0
       ENDIF
*
       IF (DVS .GE. VAR1) REMOB = 0.0
cPOTAMIN      IF (DVS .GE. 1.) REMOB = 0.0
cPOTAMIN      IF (DVS .GE. 1.6) REMOB = 0.0


*-----If harvesting takes place, weights various plant organs must be recalculated;
*          these are :TWLVG,TWSTG,TWRTG,TW
           IF(HAR .EQ. 1. AND. DAY .EQ. HARDAY) THEN
           TWLVG = FLV * TGW
           TWSTG  = FST * TGW
           TWRTG = FRT * TGW
           TW   = TGW + (TWLVD + TWSTD + TWRTD)
           ENDIF


*-----Conversion assimilated CO2 to CH2O
           GPHOT = DTGA * 30./44.


*-----Total and net growth rates
       GTW = ((REMOB*CVT) + GPHOT - TRANS - MAINT) / ASRQ
           GRT = FRT * GTW
           GST = FST * GTW
           GLV = FLV * GTW


           NGLV = GLV - DLV
           NGST = GST - DST
           NGRT = GRT - DRT


*-----Finish conditions
       IF (DVS.GT.20.0 .OR. DAY .EQ. 365.) TERMNL = .TRUE.


*-----Output section
```

```
        IF (OUTPUT) THEN
        CALL OUTDAT (2,0,'DAVTMP',DAVTMP)
        CALL OUTDAT (2,0,'DAYL  ',DAYL  )
        CALL OUTDAT (2,0,'DDTMP',DDTMP )
        CALL OUTDAT (2,0,'DPT   ',DPT   )
        CALL OUTDAT (2,0,'DTGA  ',DTGA  )
        CALL OUTDAT (2,0,'DTEFF ',DTEFF )
        CALL OUTDAT (2,0,'DVS   ',DVS   )
        CALL OUTDAT (2,0,'FGROS ',FGROS )
        CALL OUTDAT (2,0,'GPHOT ',GPHOT )
        CALL OUTDAT (2,0,'IRS   ',IRS   )
        CALL OUTDAT (2,0,'MAINT ',MAINT )
        CALL OUTDAT (2,0,'NDTUB ',NDTUB )
        CALL OUTDAT (2,0,'NGTUB ',NGTUB )
        CALL OUTDAT (2,0,'NNTUB ',NNTUB )
        CALL OUTDAT (2,0,'NTM   ',NTM   )
        CALL OUTDAT (2,0,'NTUBD ',NTUBD )
        CALL OUTDAT (2,0,'REMOB ',REMOB )
        CALL OUTDAT (2,0,'TEFF  ',TEFF  )
        CALL OUTDAT (2,0,'TGW   ',TGW   )
        CALL OUTDAT (2,0,'TGWM  ',TGWM  )
        CALL OUTDAT (2,0,'TRANS ',TRANS )
        CALL OUTDAT (2,0,'TREMOB',TREMOB)
        CALL OUTDAT (2,0,'TW    ',TW    )
        CALL OUTDAT (2,0,'TWCTUB',TWCTUB)
        CALL OUTDAT (2,0,'TWGTUB',TWGTUB)
        CALL OUTDAT (2,0,'TWLVD ',TWLVD )
        CALL OUTDAT (2,0,'TWLVG ',TWLVG )
        CALL OUTDAT (2,0,'TWNTUB',TWNTUB)
        CALL OUTDAT (2,0,'TWRTD ',TWRTD )
        CALL OUTDAT (2,0,'TWRTG ',TWRTG )
        CALL OUTDAT (2,0,'TWSTD ',TWSTD )
        CALL OUTDAT (2,0,'TWSTG ',TWSTG )
        CALL OUTDAT (2,0,'TWTUB ',TWTUB )
        CALL OUTDAT (2,0,'TWTUBD',TWTUBD)
        CALL OUTDAT (2,0,'WTMP  ',WTMP  )
        END IF

    ELSE IF (ITASK.EQ.3) THEN

*        INTEGRATION
*        =============
        DVS     = INTGRL (DVS   ,DVR   ,DELT)
        TMPSUM = INTGRL (TMPSUM,DTEFF ,DELT)
        TREMOB = INTGRL (TREMOB,REMOB ,DELT)
        TWLVD   = INTGRL (TWLVD ,DLV   ,DELT)
        TWLVG   = INTGRL (TWLVG ,NGLV  ,DELT)
        TWLVG   = AMAX1 (0.0, TWLVG)
        TWSTD   = INTGRL (TWSTD ,DST   ,DELT)
        TWSTG   = INTGRL (TWSTG ,NGST  ,DELT)
        TWSTG   = AMAX1 (0.0, TWSTG)
        WTRTD   = INTGRL (TWRTD ,DRT   ,DELT)
        TWRTG   = INTGRL (TWRTG ,NGRT  ,DELT)
        TWRTG   = AMAX1 (0.0, TWRTG)
        NTUBPD = NTUBD
        NTUBD   = INTGRL (NTUBD, (RDTU*NDTUB*TEFF),DELT)
```

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```
        NTUBD   = AMAX1 (0.0, NTUBD)
        NDTUB   = INTGRL (NDTUB, -(NTUBD-NTUBPD),DELT)
        NDTUB   = AMAX1 (0.0, NDTUB)

     ELSE IF (ITASK.EQ.4) THEN

*               TERMINAL SECTION              *
*               ===================

*-----Terminal calculations

*-----Terminal output

     CLOSE (IUNITD)

     END IF

     ITOLD = ITASK

     RETURN
     END
```

```
******************************************************************************************
***                                 3.1 ASTRO                                       ***
*---------------------------------------------------------------------------------------  *
* SUBROUTINE ASTRO                                                                       *
* Authors: Daniel van Kraalingen                                                         *
* Date   : 9 August 1987                                                                 *
* Modified by Jan Goudriaan 4 Febr 1988                                                  *
* Modified by Jan Goudriaan and Kees Spitters 7 December 1989                            *
* Purpose: This subroutine calculates astronomic daylength and photoperiodic day length  *
* (see CABO-TPE report #?) and diurnal radiation characteristics such as daily integral of *
* .sine of solar elevation, solar constant. Measured daily total of global radiation is used to find *
* atmospheric transmissivity and fraction diffuse radiation                              *
* FORMAL PARAMETERS:  (I=input,O=output,C=control,IN=init,T=time)                         *
* name          meaning                                            units    class        *
* -------       -----------                                        -------  ------        *
* DAY           Day number (Jan 1st = 1)                           -        I           *
* LAT           Latitude of the site                               degrees  I           *
* DTR           Measured daily total global radiation              J m-2 d-1  I          *
* SC            Solar constant                                     J m-2 s-1  O          *
* DS0           Daily extraterrestrial radiation                   J m-2 d-1  O          *
* SINLD         Seasonal offset of sine of solar height            -        O           *
* COSLD         Amplitude of sine of solar height                  -        O           *
* DAYL          Astronomical day length (base = 0 degrees)         h        O           *
* DSINB         Daily total of sine of solar height                s        O           *
* DSINBE        Daily total of effective solar height              s        O           *
*                                                                                        *
* FATAL ERROR CHECKS (execution terminated, message) condition                           *
*                                                                                        *
* LAT > 67, LAT < -67                                                                    *
*                                                                                        *
* SUBROUTINES and FUNCTIONS called : none                                                *
*                                                                                        *
* FILE usage : none                                                                      *
*---------------------------------------------------------------------------------------  *

      SUBROUTINE ASTRO (DAY,LAT,SC,DS0,SINLD,COSLD,
     $          DAYL,DSINB,DSINBE)
      IMPLICIT REAL (A-Z)

*-----PI and conversion factor from degrees to radians
      PARAMETER (PI=3.141592654, RAD=0.017453292)

*-----Check on input range of parameters
      IF (LATITUDEGT.67.) STOP 'ERROR IN ASTRO: LAT > 67'
      IF (LATITUDELT.-67.) STOP 'ERROR IN ASTRO: LAT <-67'

*-----Declination of the sun as function of daynumber (DAY)
      DEC = -ASIN(SIN(23.45*RAD)*COS(2.*PI*(DAY+10.)/365.))

*-----SINLD, COSLD and AOB are intermediate variables
      SINLD = SIN(RAD*LAT)*SIN(DEC)
      COSLD = COS(RAD*LAT)*COS(DEC)
      AOB   = SINLD/COSLD

*-----Daylength (DAYL)
      DAYL  = 12.0*(1.+2.*ASIN(AOB)/PI)
```

```
      DSINB = 3600.*(DAYL*SINLD+24.*COSLD*SQRT(1.-AOB*AOB)/PI)
      DSINBE= 3600.*(DAYL*(SINLD+0.4*(SINLD*SINLD+COSLD*COSLD*0.5))+
     $      12.0*COSLD*(2.0+3.0*0.4*SINLD)*SQRT(1.-AOB*AOB)/PI)

*-----Solar constant (SC) and daily extraterrestrial (DS0)
      SC  = 1370.*(1.+0.033*COS(2.*PI*DAY/365.))
      DS0 = SC*DSINB
      RETURN
      END
```

```
***************************************************************************************
***                            3.2 TOTASS                                         ***
*-------------------------------------------------------------------------------------*
* SUBROUTINE TOTASS                                                                   *
* Authors: Daniel van Kraalingen                                                      *
* Date   : 1 December 1987                                                            *
* Modified by Jan Goudriaan 5-Febr-1988                                               *
* Modified by Jan Goudriaan and Kees Spitters 7 December 1989                         *
* Units modified by Elly Best & Will Boyd 28 July 1995                                *
* Purpose: This subroutine calculates daily total gross assimilation (DTGA) by        *
* performing a Gaussian integration over time. At three different times of the day,   *
*..radiation is computed and used to determine assimilation whereafter integration    *
* takes place.(Source: Post-graduate Course 'Simulation of plant growth and crop      *
* production. Pontignano, Siena, Italy; 3-12 November, 1992. Dept. Theor.             *
* Production Ecol. (TPE-WAU), Wageningen Agricultural University, and DLO-Centre       *
* for Agrobiological Research (CABO-DLO).)                                             *
*                                                                                     *
* FORMAL PARAMETERS:  (I=input,O=output,C=control,IN=init,T=time)                     *
* name           meaning                                              units    class  *
* ------         ----------                                           -------  ------- *
* SC             Solar constant                                       J m-2 s-1  I     *
* DAYL           Day length (base = 0 degrees)                        h          I     *
* SINLD          Intermediate variable in calculating solar declination  -       I     *
* COSLD          Intermediate value in calculating solar height        -        I     *
* DSINBE         Daily total of effective solar height                 s        I     *
* DTR            Measured daily total of global radiation              J m-2 d-1  I     *
* RC             Reflection coefficient of irradiation at water surface (relative)  -  I  *
* L              Water type specific light extinction coefficient      -        I     *
* K              Plant species specific light extinction coefficient   -        I     *
* AMAX           Assimilation rate at light saturation for individual shoots g CO2/g DW/h  I  *
* EE             Initial light use efficiency for individual shoots    g CO2 J-1  I     *
* TL             Thickness per plant layer                             m        I     *
* DPT            Water depth                                           m        I     *
* RCHSHST        Relation coefficient shoot weight-stem length         m g DW-1   I     *
* TGW            Total live plant dry weight                           g DW m-2   I     *
* FGROS          Instantaneous assimilation rate of whole canopy       g CO2/m2 soil/h  O  *
* FL             Leaf dry matter allocation to each layer of plant     -        I     *
* FLV            Fraction of total dry matter increase allocated to leaves  -    I     *
* FRT            Fraction of total dry matter increase allocated to roots  -     I     *
* FST            Fraction of total dry matter increase allocated to stems  -     I     *
* WLV            Dry weight of leaves                                  g DW m-2   I     *
* WST            Dry weight of stems                                   g DW m-2   I     *
* HAR            Harvesting                                            -        I     *
* HARDAY         Harvesting day number                                 d        I     *
* HARDEP         Harvesting depth                                      m        I     *
* DTGA           Daily total gross assimilation                        g CO2 m-2 d-1  O  *
* NPL            Plant density                                         plants m-1  I    *
* IRS            Total irradiance just under the water surface         J m-2.s-1  I     *
* REMOB          Remobilization rates of carbohydrates                 g DW m-2 d-1  I   *
* TWLVG          Total dry weight of live leaves                       g DW m-2  I      *
* TWSTG          Total dry weight of live stems                        g DW m-2  I      *
* TWRTG          Total dry weight of live roots                        g DW m-2  I      *
* SURFAC         Expression of warning that plant canopy is not at      -               *
*                surface and tuber class has died                                      *
* CRIFAC         Critical weight per 0.1 m plant layer                 gDW/0.1 m  I      *
*                                                                      plnt ht per plnt *
```

```
*                                                                      *
*  SUBROUTINES and FUNCTIONS called : ASSIM                            *
*                                                                      *
*  FILE usage : none                                                   *
*----------------------------------------------------------------------*

      SUBROUTINE TOTASS (SC,DAYL,SINLD,COSLD,DSINBE,DTR,RC,L,K,
     $          AMAX,EE,TL,DPT,RCSHST,TGW,FGROS,FL,
     $          FLV,FRT,FST,WLV,WST,DAY,HAR,HARDAY,
     $          HARDEP,DTGA,NPL,IRS,REMOB,TWLVG,TWSTG,
     $          TWRTG,SURFAC,CRIFAC)

      IMPLICIT REAL(A-Z)
      REAL XGAUSS(3), WGAUSS(3)
      INTEGER II, IGAUSS

      PARAMETER (PI=3.141592654)

      DATA IGAUSS /3/
      DATA XGAUSS /0.1127, 0.5000, 0.8873/
      DATA WGAUSS /0.2778, 0.4444, 0.2778/

*-----Assimilation set to zero & three different times of the day (HOUR)
      DTGA = 0.
      DO 10 II=1,IGAUSS

*-----At the specified HOUR, radiation is computed and used to compute assimilation
      HOUR = 12.0+DAYL*0.5*XGAUSS(II)

*-----Sine of solar elevation
      SINB = AMAX1(0.,SINLD+COSLD*COS(2.*PI*(HOUR+12.)/24.))

*-----Diffuse light fraction (FRDIF) from atmospheric transmission (ATMTR)
      PAR   = 0.5*DTR*SINB*(1.+0.4*SINB)/DSINBE
      ATMTR = PAR/(0.5*SC*SINB)
      FRDIF = 1.47-1.66*ATMTR
      IF (ATMTR.LE.0.35.AND.ATMTR.GT.0.22) FRDIF=1.-6.4*(ATMTR-0.22)**2
      IF (ATMTR.LE.0.22) FRDIF=1.
      FRDIF = AMAX1(FRDIF,0.15+0.85*(1.-EXP(-0.1/SINB)))

*-----Diffuse PAR (PARDIF) and direct PAR (PARDIR)
      PAR   = 0.5*DTR*SINB*(1.+0.4*SINB)/DSINBE
      PARDIF = MIN (PAR,SINB*FRDIF*ATMTR*0.5*SC)
      PARDIR = PAR-PARDIF

      CALL ASSIM
     $ (PARDIR,PARDIF,RC,L,K,AMAX,EE,TL,DPT,RCSHST,TGW,
     $ FL,FLV,FRT,FST,WLV,WST,DAY,HAR,HARDAY,HARDEP,II,FGROS,NPL,IRS,
     $ REMOB,TWLVG,TWSTG,TWRTG,SURFAC,CRIFAC)

*-----Integration of assimilation rate to a daily total (DTGA)
      DTGA = DTGA+FGROS*WGAUSS(II)
10    CONTINUE

      DTGA = DTGA*DAYL
```

```
      RETURN
      END


*****************************************************************************************
***                              3.3 ASSIM                                          ***
*_____*
*                                                                                     *
*                                                                                     *
* Authors: Elly Best & Will Boyd                                                      *
* Date   : 28 July 1995                                                               *
*  Purpose: This subroutine performs an instantaneous calculation of light profile   *
*    in the water column, light absorbed for photosynthesis, and                     *
*    assimilation at all these depth layers. The depth-integrated variable is FGROS. At *
*    harvesting, the plant material is removed per depth layer from the existing biomass *
*                                                                                     *
*                                                                                     *
* FORMAL PARAMETERS:  (I=input,O=output,C=control,IN=init,T=time)                     *
* name          meaning                                              units    class  *
* ------        ----------                                           -------  ------ *
* PARDIR        Instantaneous flux of direct radiation (PAR)         W m-2    I      *
* PARDIF        Instantaneous flux of diffuse radiation(PAR)         W m-2    I      *
* RC            Reflection coefficient of irradiation at water surface  -       I      *
* L             Water type specific light extinction coefficient     m-1      I      *
* K             Plant species specific light extinction coefficient  m2 g-1DW  I      *
* AMAX          Assimilation rate at light saturation for individual shoots  g CO2/g DW/h I *
* EE            Initial light use efficiency for individual shoots    g CO2 J-1I       *
* TL            Thickness per plant layer                            m        I      *
* DPT           Water depth                                          m        I      *
* RCHSHST       Relation coefficient tuber weight-stem length        m/g DW   I      *
* TGW           Total live plant dry weight                          g DW m-2 I      *
* FL            Leaf dry matter allocation to each layer of plant    -        I      *
* FLV           Fraction of total dry matter increase allocated to leaves  -     I      *
* FST           Fraction of total dry matter increase allocated to stems   -     I      *
* WLV           Dry weight of leaves                                 g DW m-2 I      *
* WST           Dry weight of stems                                  g DW m-2 I      *
* HAR           Harvesting                                           -        I      *
* HARDAY        Harvesting day number                                d        I      *
* HARDEP        Harvesting depth                                     m        I      *
* II            Counter in DO LOOP, indicates 1 of 3 times per day (HOUR)  -     I      *
* FGROS         Instantaneous assimilation rate of the plant         g CO2/m2/h  O      *
* NPL           Plant density                                        plants m-2  I      *
* IRS           Total irradiance just under the water surface        J m-2 s-1 I      *
* REMOB         Remobilization rates of carbohydrates                g DW m-2 d-1 I      *
* TWLVG         Total dry weight of live leaves                      g DW m-2 I      *
* TWSTG         Total dry weight of live stems                       g DW m-2 I      *
* TWRTG         Total dry weight of live roots                       g DW m-2 I      *
* SURFAC        Expression of warning that plant canopy is not at    -               *
*               water surface and tuber class has died                               *
* CRIFAC        Critical weight per 0.1 m plant layer                gDW/0.1 m I      *
*                                                                   plnt ht per plnt  *
*                                                                                     *
*                                                                                     *
* SUBROUTINES called : none                                                          *
* FUNCTIONS called : AFGEN                                                            *
*                                                                                     *
*                                                                                     *
* FILE usage : none                                                                  *
*_____*
```

```
      SUBROUTINE ASSIM (PARDIR,PARDIF,RC,L,K,AMAX,EE,TL,
     $           DPT,RCSHST,TGW,FL,FLV,FRT,FST,
     $           WLV,WST,DAY,HAR,HARDAY,HARDEP,II,
     $           FGROS,NPL,IRS,REMOB,TWLVG,TWSTG,
     $           TWRTG,SURFAC,CRIFAC)

      IMPLICIT REAL(A-Z)
      REAL DMPC(5), SC(100), IRZ(100) , IABS(100), IABSL(100)
      REAL HIG(100), AH(100), REDF(100), SumZ
      INTEGER IMN1, IRED, I, LOOP, Layers, LBelow, ILAY, II, MM
      PARAMETER (IMN1  = 40)
      REAL REDFT(IMN1), DMPCT(IMN1)

*-----Read AFGEN functions
      CALL RDAREA ('REDFT ',REDFT ,IMN1 ,IRED )
      CALL RDAREA ('DMPCT ',DMPCT, IMN1 ,ILAY )

*-----Irradiation just beneath the water surface
      IRS = PARDIR + PARDIF
      IRZ(1) = IRS * (1.0 - RC)

*-----Set a critical shoot weight for each depth layer
      CRIGWT = CRIFAC * NPL

*-----Canopy assimilation is set to zero
      FGROS = 0.

*-----Calculate stem length
      STEMLE = AMIN1(DPT+.0995, (RCSHST*(WLV+WST)))

*-----Calculate shoot biomass
      SHTBIO = TWLVG + TWSTG

      IF (STEMLE .GT. DPT+.08)THEN

*-----Determine total number of layers in the given water depth
      LOOP = INT (DPT/TL + 0.1) + 1

*-----Water depth must be > 0.8m to use this distribution
*     method; otherwise, go to ELSE which will distribute biomass equally
      IF (LOOP .GT. 9) THEN

*-----If the biomass per layer is > or = the critical weight, proceed as usual
      IF ((SHTBIO/(LOOP-1)) .GE. CRIGWT) THEN

*-----Since plant biomass has reached the surface REMOB becomes zero
      REMOB = 0.0
      SURFAC = 1.

*-----Initialize variable for sum of percent biomass in 1st 5 layers
      FIRST5 = 0.0

*-----Distribute 78.4 percent of total plant biomass in 1st 5 layers
**      write(*,*)' Total weight = ',TGW
      DO 10 I = 1,5
      VAL = REAL (I)
```

```
      DMPC(I) = LINT (DMPCT,ILAY,VAL)


*-----Sum of percent biomass in the 1st 5 layers
      FIRST5 = FIRST5 + DMPC(I)
      SC(I) = TGW * DMPC(I)
**      write(*,*)' layer ',I,' = ',SC(I)
   10 CONTINUE


*-----Determine percent biomass distributed over the lower layers
      PCTLOW = 1.0 - (FIRST5 + FRT)


*-----Distribute 13 percent of biomass in the lower layers (excluding last layer)
*      with biomass gradually decreasing toward the bottom
*      LOOP (integer) .. Number of 0.1m water layers
*      LAYERS (integer) .. Layers remaining after initial 5
*-----SUMZ (real) .. Summation of layers 6 through LOOP
*-----LBELOW (integer) .. Layer number going from bottom to top

*-----6 Is the 1st 5 layers + the bottom 1 layer (roots)

      LAYERS = LOOP - 6
      SUMZ = (LAYERS/2.0) * (LAYERS+1.0)

      DO 20 I = 6,LOOP-1
      LBELOW = LAYERS - (I-5) + 1.0
      SC(I) = (LBELOW/SUMZ) * (TGW * PCTLOW)
   20 CONTINUE
*-----If not enough biomass per layer .. take away layers until enough
      ELSE

      LESS = 1
   23 LESS = LESS + 1


*-----Initialize all layers at 0.0
      DO 25 MM = 1,LOOP-1
        SC(MM) = 0.0
   25 CONTINUE


*-----If critical biomass is not met ... go back to 23 & remove a layer
      IF ((SHTBIO/(LOOP-LESS)).LT.CRIGWT .AND. LOOP-LESS.GT.1)GOTO 23


*-----Otherwise distribute shoot biomass over the layers it can reach
*-----Loop goes from bottom to top ... i.e. 10,9,8, ...,2,1
      SURFAC = 0.
      DO 27 MM = LOOP-1,LESS,-1
        SC(MM) = AMIN1(CRIGWT, SHTBIO)
        IF (SHTBIO .GT. CRIGWT) SC(MM-1) = SHTBIO - CRIGWT
        IF (SHTBIO .GT. CRIGWT) SHTBIO = SHTBIO - CRIGWT
   27 CONTINUE

      ENDIF

      ELSE

*-----If water depth is 0.8m or less, plant biomass is distributed evenly over the existing layers
```

A20

```
*-----If biomass reaches the surface ... proceed as usual
      IF (SHTBIO/(LOOP-1) .GE. CRIGWT) THEN
      SURFAC = 1.
      DO 32 I = 1,LOOP-1
      SC(I) = SHTBIO/(LOOP-1)
**       write(*,*)' layer ',I,' = ',SC(I)
   32 CONTINUE

      ELSE
*-----If biomass does not reach the surface

      LESS = 1
   33 LESS = LESS + 1

*-----Initialize all layers at 0.0
      DO 35 MM = 1,LOOP-1
        SC(MM) = 0.0
   35 CONTINUE

*-----If critical biomass is not met ... go back to 33 & remove a layer
      IF ((SHTBIO/(LOOP-LESS)).LT.CRIGWT .AND. LOOP-LESS.GT.1)GOTO 33

*-----Otherwise distribute shoot biomass over the layers it can reach
*-----Loop goes from bottom to top ... i.e. 8,7,6, ...,2,1
      SURFAC = 0.
      DO 37 MM = LOOP-1,LESS,-1
        SC(MM) = AMIN1(CRIGWT, SHTBIO)
        IF (SHTBIO .GT. CRIGWT) SC(MM-1) = SHTBIO - CRIGWT
        IF (SHTBIO .GT. CRIGWT) SHTBIO = SHTBIO - CRIGWT
   37 CONTINUE

CC    DO 38 MM = 1,LOOP-1
CC      write(*,*)' layer = ',MM,'  biomass = ',SC(MM)
CC  38 CONTINUE
CC    read(*,*)

      ENDIF

      ENDIF

*-----Distribute 8.6 percent of biomass in the last layer (roots)
      SC(LOOP) = TWRTG
**       write(*,*)' layer ',LOOP,' = ',SC(LOOP)
**       read(*,*)

*-----Harvesting
      IF (HAR .EQ. 1. .AND. DAY .EQ. HARDAY)THEN
      IF (HARDEP .GT. DPT) HARDEP = DPT
      DO 45 I = 1,(HARDEP/TL+1.0)
      SC(I) = 0.0
   45 CONTINUE

*-----Reset total live weight (TGW) to zero
      IF(II .EQ. 1)TGW = 0.0
      ENDIF
```

```
      DO 60 I = 1,LOOP

*-----Total irradiation on top of stratum I
      IRZ(I+1) = IRZ(I) * EXP(-TL* L - K* SC(I))
      IF(SC(I) .EQ. 0.0) GOTO 48

*-----Radiation absorbed by macrophyte community
      IABS(I) = (IRZ(I)-IRZ(I+1))*SC(I)*K/(K*SC(I)+TL*L)

*-----Radiation absorbed by leaves, excluding bottom layer
      IF(I .LT. LOOP) IABSL(I) = IABS(I) * FL
      IF(IABSL(I) .EQ. 0.0)GOTO 48

*-----Height on top of stratum I measured from the water surface
      HIG(I) = TL * (LOOP - I)

*-----Absolute height of vegetation on top of stratum I, measured
*     from the top of the plant
      AH(I) = STEMLE - HIG(I)

*-----Reduction factor over the vertical of the vegetation
      REDF(I) = LINT(REDFT,IRED,AH(I))

*-----Instantaneous CO2 assimilation rate per depth layer
      FGL = SC(I)*AMAX*REDF(I)*(1.-EXP(-EE*IABSL(I)*3600. /
     $ (AMAX*REDF(I)*SC(I))))
      GOTO 50
   48 FGL = 0.0
   50 FGROS = FGROS + FGL

*-----If plants are harvested, live plant weight is recalculated
      IF (HAR.EQ.1 .AND. DAY.EQ.HARDAY .AND. II.EQ.1) THEN
      TGW = TGW + SC(I)
      ENDIF
   60 CONTINUE
      ENDIF

      RETURN
      END
```

```
*----------------------------------------------------------------------*
* Model data file generated by FST translator version 1.15 TEST        *
* contains:                                                            *
* - Initial constants as far as specified with INCON statements,       *
* - Model parameters,                                                  *
* - AFGEN functions,                                                   *
* - A SCALE array in case of a general translation                     *
*                                                                      *
* File name: MODELP0.DAT; input MODEL.DAT file for calibration run of POTAM  *
* Calibration data Zandvoort Canals (Appendix C); weather file NLD4.987 pertaining  *
*  to De Bilt, The Netherlands, 1987. LT=1.07; air temperature         *
* Date: 24 January 2000                                                *
* Time: 17:00:00                                                       *
*----------------------------------------------------------------------*
```

```
* Initial constants
* _____
INTUB  = 0.083
IREMOB = 0.
IWLVD  = 0.
IWLVG  = 0.
IWRTD  = 0.
IWRTG  = 0.
IWSTD  = 0.
IWSTG  = 0.
NUL    = 0.
REMOB  = 0.0


* Model parameters
* _____
YRNUM  = 1.
AMX    = 0.019
CRIFAC = 0.0076
CVT    = 1.05
DAYEM  = 1.
DELAY  = 7.
EE     = 0.000011
HAR    = 0.
HARDAY = 304.
HARDEP = 0.8
NDTUB  = 240.
NINTUB = 8.
NPL    = 30.
RC     = 0.06
RCSHST = 12.0
RDTU   = 0.026
REDAM  = 1.
ROC    = 0.0576
RTR    = .19
SURPER = 27.
TBASE  = 3.
TL     = 0.1
TWCTUB = 19.92

* AFGEN functions
* _____
* AMDVST =
*    0.001, 1.,
*    1.243, 1.,
*    1.244, 0.6,
*    20.0, 0.6

AMTMPT =
   -30., 0.00001,
   0., 0.00001,
   10., 0.027,
   18., 0.51,
   20., 0.53,
   23., 0.71,
   28., 0.91,
```

```
   30., 1.0,
   50., 0.00001

DMPCT =
   1.0, .043,
   2.0, .043,
   3.0, .231,
   4.0, .254,
   5.0, .213

DPTT =
   1., 1.3,
   365., 1.3

* DVRVT  =
*  -15., 0.,
*    0., 0.,
*   30.,0.015
* DVRRT  =
*  -15., 0.,
*    0., 0.,
*   30.,0.040

FLT   =
   0., 0.8,
   3.5, 0.8,
   20.0, 0.8

FLVT  =
   0., 0.731,
   3.5, 0.731,
   20.0, 0.731

 FSTT  =
   0., 0.183,
   3.5, 0.183,
   20.0, 0.183

FRTT  =
   0., 0.086,
   3.5, 0.086,
   20.0, 0.086

KT   =
   0., 0.095,
   3.5, 0.095,
   20.0, 0.095

LT   =
   1., 1.07,
   365., 1.07

RDRT  =
   0., 0.047,
   19., 0.047,
   30., 0.094,
```

```
   40., 0.188,
   50., 1.

RDST  =
   0., 0.047,
   19., 0.047,
   30., 0.094,
   40., 0.188,
   50., 1.

REDFT =
   0.0, 1.0,
   1.0, 1.0,
   5.0, 1.0

TEFFT =
   0.0, 0.0001,
   10., 0.5,
   20., 1.,
   30., 2.,
   40., 4.,
   45., 6.,
   50., 0.0001


WTMPT =
   1., 0.,
   365., 0.

NTMT  =
   1., 400.,
   98., 400.,
   134., 400.,
   190., 400.,
   233., 400.,
   260., 400.,
   289., 400.,
   365., 400.

TGWMT =
   1., 0.,
   98., 0.64,
   134., 8.,
   190., 50.0,
   233., 78.5,
   260., 52.0,
   289., 29.5,
   365., 0.
```

```
*-----------------------------------------------------------------------*
* TIMER file contains                                                    *
*                                                                        *
* - The used DRIVER and TRACE in case of GENERAL translation             *
* - The TIMER variables used in both translation modes                   *
* - Additional TIMER variables in case of GENERAL translation            *
```

```
* - The WEATHER control variables if weather data are used          *
* - Miscellaneous FSE variables in case of FSE translation          *
*                                                                   *
* File: POTAM.FOR                                                   *
* Date: 09-08-97                                                    *
* Time: 15:40:06                                                    *
* TIMER variables used in GENERAL and FSE translation modes         *
* ----------------------------------------------------------------- *
STTIME      = 1.    ! start time
FINTIM      = 365.  ! finish time
DELT        = 1.    ! time step (for Runge-Kutta first guess)
PRDEL       = 1.    ! output time step
IPFORM      = 4     ! code for output table format:
                    ! 4 = spaces between columns
                    ! 5 = TAB's between columns (spreadsheet output)
                    ! 6 = two column output

                    ! The string array PRSEL contains the output variables for which
                    ! formatted tables have to be made. One or more times there is a
                    ! series of variable names terminated by the word <TABLE>.
                    ! The translator writes the variables in each PRINT statement to
PRSEL       =       ! a separate table.
* 'DAVTMP',
* 'DAYL  ',
* 'DDTMP ',
* 'DTEFF ',
* 'DTGA  ',
* 'DVS   ',
* 'FGROS ',
* 'GPHOT ',
* 'IRS   ',
* 'MAINT ',
  'NDTUB ',
* 'NGTUB ',
* 'NNTUB ',
* 'NTM   ',
* 'NTUBD ',
* 'NTUBPD',
* 'REMOB ',
* 'TEFF  ',
  'TGW   ',
* 'TGWM  ',
* 'TMPSUM',
* 'TRANS ',
* 'TREMOB',
* 'TW    ',
* 'TWGTUB',
* 'TWLVD ',
* 'TWLVG ',
* 'TWNTUB',
* 'TWRTD ',
  'TWRTG ',
* 'TWSTD ',
* 'TWSTG ',
* 'TWTUB ',
* 'TWTUBD',
```

```
*"WTMP ',
     '<TABLE>'
  COPINF = 'N'             ! Switch variable whether to copy the input files
                           ! to the output file ('N' = do not copy,
                           ! 'Y' = copy)
  DELTMP = 'N'  ! Switch variable what should be done with the
                           ! temporary output file ('N' = do not delete,
                           ! 'Y' = delete)
  IFLAG  = 1101 ! Indicates where weather error and warnings
                           ! go (1101 means errors and warnings to log
                           ! file, errors to screen, see FSE manual)
*IOBSD = 1991,182  ! List of observation data for which output is
                           ! required. The list should consist of pairs
                           ! <year>,<day> combination


WEATHER control variables
-------------------------
  WTRDIR      = 'C:\SYS\WEATHER\'
  CNTR        = 'NLD'       ! Country code
  ISTN        = 4           ! Station code
  IYEAR       = 1978        ! Year



*_____*
*                                                                         *
* CONTROL.DAT file contains:                                              *
* File names to be used by FSE 2.1                                        *
* The input files (except FILEIR) may be used in reruns.                  *
* Up to five input data files may be used (FILEI1-5)                      *
*_____*

  FILEON = 'RES.DAT'         ! Normal output file
  FILEOL = 'MODEL.LOG'       ! Log file
  FILEIR = 'RERUNS.DAT'      ! Reruns file
  FILEIT = 'TIMER.DAT'       ! File with timer data
  FILEI1 = 'MODEL.DAT'       ! First input data file

* FILEI2 = ' '               ! Second input data file (not used)
* FILEI3 = ' '               ! Third input data file (not used)
* FILEI4 = ' '               ! Fourth input data file (not used)
* FILEI5 = ' '               ! Fifth input data file (not used)
```

Appendix B
Variable Listing

Abbreviation	Explanation	Dimension
AH(i)	Absolute height of vegetation on top of stratum I, measured from the plant top	m
AMAX	Actual CO_2 assimilation rate at light saturation for individual shoots	g CO_2.g DW^{-1}.h^{-1}
AMTMP	Daytime temperature effect on AMX (relative)	-
AMTMPT	Table of AMX as function of DVS	-, -
AMX	Potential CO_2 assimilation rate at light saturation for shoot tips	g CO_2.g DW^{-1}.h^{-1}
ASRQ	Assimilate requirement for plant dry matter production	g CH_2O.g DW^{-1}
ATMTR	Atmospheric transmission coefficient	-
COSLD	Intermediate variable in calculating solar height	-
CRIFAC	Critical weight per 0.1 m vegetation layer	g DW per 0.1 m plnt ht^{-1}. $plnt^{-1}$
CRIGWT	Critical weight per 0.1 m vegetation layer	g DW per 0.1 m plnt ht^{-1}. m^{-2}
CVT	Conversion factor of translocated dry matter into CH_2O	-
DAVTMP	Daily average temperature	°C
DAY	Day number (January 1=1)	d
DAYEM	First Julian day number	d
DAYL	Day length	h
DDELAY	Integer value of DELAY	-
DDTMP	Daily average daytime temperature	°C
DEC	Declination of the sun	radians
DELAY	Lag period chosen to relate water temperature to air temp., in cases where water temp. has not been measured	d
DEPTH	Water depth	m
DLV	Death rate of leaves	g DW. m^{-2}.d^{-1}
DMPC(i)	Dry matter allocation to each plant layer (relative)	-
DMPCT	Table to read DMPC(i) as function of depth layer (relative)	-
DPTT	Table to read water depth as a function of day no	m, d
DRT	Death rate of roots	g DW. m^{-2}.d^{-1}
DSINB	Integral of SINB over the day	s.d^{-1}
DSINBE	Daily total of effective solar height	s.d^{-1}
DSO	Daily extra-terrestrial radiation	J.m^{-2}.d^{-1}
DST	Death rate of stems	g DW.m^{-2}.d^{-1}
DTEFF	Daily effective temperature	°C
DTGA	Daily total gross CO_2 assimilation of the vegetation	g CO_2.m^{-2}.d^{-1}
DTR	Measured daily total global radiation	J.m^{-2}.d^{-1}
DVR	Development rate as function of temperature sum	d^{-1}

DVRRT	Table of post-anthesis development rate as function of temperature sum (used for calibration; not read from MODEL.DAT)	$d^{-1}, {}^{\circ}C$
DVRVT	Table of pre-anthesis development rate as function of temperature sum (used for calibration; not read from MODEL.DAT)	$d^{-1}, {}^{\circ}C$
DVRVT	Development rate pre-anthesis	d^{-1}
DVS	Development phase of the plant	-
EE	Initial light use efficiency for shoots	$g\ CO_2 . J^{-1}$
FGROS	Instantaneous CO_2 assimilation rate of the vegetation	$g\ CO_2.m^{-2}.h^{-1}$
FGL	Instantaneous CO_2 assimilation rate per vegetation layer	$g\ CO_2.m^{-2}.h^{-1}$
FL	Leaf dry matter allocation to each layer of shoot (relative)	-
FLT	Table to read FL as function of DVS	-, -
FLV	Fraction of total dry matter increase allocated to leaves	-
FLVT	Table to read FLV as function of DVS	-
FRDIF	Diffuse radiation as a fraction of total solar radiation	-
FRT	Fraction of total dry matter increase allocated to roots	-
FRTT	Table to read FRT as function of DVS	-, -
FST	Fraction of total dry matter increase allocated to stems	-
FSTT	Table to read FST as function of DVS	-, -
GLV	Dry matter growth rate of leaves	$g\ DW.m^{-2}.d^{-1}$
GPHOT	Daily total gross assimilation rate of the vegetation	$g\ CH_2O.m^{-2}.d^{-1}$
GRT	Dry matter growth rate of roots	$g\ DW.m^{-2}.d^{-1}$
GST	Dry matter growth rate of stems	$g\ DW.m^{-2}.d^{-1}$
GTW	Dry matter growth rate of the vegetation (plant excluding tubers)	$g\ DW.m^{-2}.d^{-1}$
HAR	Harvesting (0=no harvesting, 1=harvesting)	-
HARDAY	Harvesting day number	d
HARDEP	Harvesting depth (measured from water surface)	m
HIG(i)	Height on top of stratum I (measured from water surface)	m
HOUR	Selected hour during the day	h
I	Counter in DO LOOP	-
IABS(i)	Total irradiance absorbed per depth layer	$J.m^{-2}.s^{-1}$
IABSL(i)	Total irradiance absorbed per depth layer	$J.m^{-2}.s^{-1}$
IDAY	Integer equivalent of variable DAY	d
INTUB	Initial dry weight of a tuber	$g\ DW.tuber^{-1}$
IREMOB	Initial value remobilization	$g\ CH_2O.m^{-2}$
IRS	Total irradiance just under the water surface	$J.m^{-2}.s^{-1}$
IRZ(i)	Total irradiance on top of depth layer I	$J.m^{-2}.s^{-1}$
IWLVD	Initial dry matter of dead leaves	$g\ DW.m^{-2}$
IWLVG	Initial dry matter of green (live) leaves	$g\ DW.m^{-2}$
IWRTD	Initial dry matter of dead roots	$g\ DW.m^{-2}$
IWRTG	Initial dry matter of green (live) roots	$g\ DW.m^{-2}$
IWSTD	Initial dry matter of dead stems	$g\ DW.m^{-2}$
IWSTG	Initial dry matter of green (live) stems	$g\ DW.m^{-2}$
K	Plant species specific light extinction coefficient	$m^2.g\ DW^{-1}, -$
KCOUNT	Counter used to calculate number of consecutive days in which plantlets have a negative net photosynthesis	-
KT	Table to read K as function of DVS	-
L	Water type specific light extinction coefficient	m^{-1}
LAT	Latitude of the site	degrees
LT	Table to read L as function of day number	d, m^{-1}
MAINT	Maintenance respiration rate of the vegetation	$g\ CH_2O.m^{-2} \cdot d^{-1}$
MAINTS	Maintenance respiration rate of the vegetation at reference temperature	$g\ CH_2O.m^{-2} \cdot d^{-1}$
NDTUB	Dormant tuber number	$dormant\ tubers.m^{-2}$

NGLV	Net growth rate of leaves	$g\ DW.m^{-2}.d^{-1}$
NGRT	Net growth rate of roots	$g\ DW.m^{-2}.d^{-1}$
NGST	Net growth rate of stems	$g\ DW.m^{-2}.d^{-1}$
NGTUB	Sprouting tuber number	$spr.\ tubers.m^{-2}$
NINTUB	Tuber number concurrently initiated per plant	$conc.in.tubers\ .plnt^{-1}$
NNTUB	New tuber number	$new\ tubers\ .m^{-2}$
NPL	Plant density	$plants\ .m^{-2}$
NTM	Tuber density measured (field site)	$tubers.m^{-2}$
NTMT	Table to read NTM as function of day number	$tubers.m^{-2},\ d$
NTUBD	Dead tuber number	$dead\ tubers.m^{-2}$
NUL	Zero (0)	-
NTUBPD	Dead tuber number previous day	$dead\ p.d.tubers.m^{-2}$
PAR	Instantaneous flux of photosynthetically active radiation	$J.m^{-2}.s^{-1}$
PARDIF	Instantaneous flux of diffuse PAR	$J.m^{-2}.s^{-1}$
PARDIR	Instantaneous flux of direct PAR	$J.m^{-2}.s^{-1}$
PI	Ratio of circumference to diameter of circle	-
RAD	Factor to convert degrees to radians	$radians.degree^{-1}$
RC	Reflection coefficient of irradiance at water surface (relative)	-
RCSHST	Relation coefficient tuber weight-stem length	$m.g\ DW^{-1}$
RDR	Relative death rate of leaves (on DW basis)	d^{-1}
RDRT	Table to read RDR as function of DAVTMP	$d^{-1},\ {}^{o}C$
RDS	Relative death rate of stems and roots (on DW basis)	d^{-1}
RDST	Table to read RDS as function of DAVTMP	$d^{-1},\ {}^{o}C$
RDTU	Relative death rate of tubers (on number basis)	d^{-1}
REDAM	Reduction factor to relate AMX to pH and oxygen levels of the water (relative)	-
REDF(i)	Reduction factor for AMX to account for senescence plant parts over vertical axis of vegetation (relative)	-
REMOB	Remobilization rate of carbohydrates	$g\ DW.m^{-2}.d^{-1}$
ROC	Relative conversion rate of tuber into plant material	$g\ CH_2O.g\ DW^{-1}.d^{-1}$
RTR	Maximum relative tuber growth rate at 20° C	$g\ DW.tuber^{-1}.d^{-1}$
RTRL	Relative tuber growth rate at ambient temperature	$g\ DW.tuber^{-1}.d^{-1}$
SC	Solar constant corrected for varying distance sun-earth	$J.m^{-2}.s^{-1}$
SC(i)	Shoot dry matter in depth layer i	$g\ DW.m^{-2}.layer^{-1}$
SHTBIO	Shoot biomass; one term for sum WLV + WST	$g\ DW.\ m^{-2}$
SINB	Sine of solar elevation	-
SINLD	Intermediate variable in calculating solar declination	-
STEMLE	Stem length	m
SURFAC	Expression of warning that plant canopy is not at water and tuber class has died	-
SSURPR	Integer value of SURPER	-
SURPER	Survival period sprouting tubers	d
TBASE	Base temperature for juvenile plant growth	^{o}C
TEFF	Factor accounting for effect of temperature on maintenance respiration, remobilization, relative tuber growth and death rates	-
TEFFT	Table to read TEFF as function of temperature (Q10 of 2, up to 45 ^{o}C)	$-,\ {}^{o}C$
TGW	Total live plant dry weight (excluding tubers)	$g\ DW.m^{-2}$
TGWM	Total live plant dry weight measured (field site)	$g\ DW.m^{-2}$
TGWMT	Table to read TGWM as function of day number	$g\ DW.m^{-2},\ d$
TL	Thickness per depth layer	m
TMAX	Daily maximum temperature	^{o}C
TMIN	Daily minimum temperature	^{o}C
TMPSUM	Temperature sum after 1 January	^{o}C
TRANS	Translocation rate of carbohydrates	$g\ CH_2O.m^{-2}.d^{-1}$

TREMOB	Total remobilization	g DW.m^{-2}
TW	Total live + dead plant dry weight (excluding tubers)	g DW.m^{-2}
TWCTUB	Total critical dry weight of new tubers	g DW.m^{-2}
TWGTUB	Total dry weight of sprouting tubers	g DW.m^{-2}
TWLVD	Total dry weight of dead leaves	g DW.m^{-2}
TWLVG	Total dry weight of live leaves	g DW.m^{-2}
TWNTUB	Total dry weight of new tubers	g DW.m^{-2}
TWRTD	Total dry weight of dead roots	g DW.m^{-2}
TWRTG	Total dry weight of live roots	g DW.m^{-2}
TWSTD	Total dry weight of dead stems	g DW.m^{-2}
TWSTG	Total dry weight of live stems	g DW.m^{-2}
TWTUB	Total dry weight of tubers	g DW.m^{-2}
WLV	Dry weight of leaves (live + dead)	g DW.m^{-2}
WRT	Dry weight of roots (live + dead)	g DW.m^{-2}
WST	Dry weight of stems (live + dead)	g DW.m^{-2}
WTMP	Daily water temperature	°C
WTMPT	Table to read WTMP as function of day number	°C, d
YRNUM	Year number simulation (1-5)	y

Appendix C
Manipulation of Literature Data Used for the Model Equations[1]

Introduction

A 3-year study (1985-87) was conducted to determine the characteristics of biomass and photosynthetic activity of a sago pondweed population in The Netherlands. The collected data were meant to be used as a basis for the development of a dynamic numerical model to simulate the growth of sago pondweed populations in changing environmental and latitudinal conditions. The collected data have so far not been published, because of time constraints of the first author.

Site Characteristics

The site of study for the sago pondweed populations is located in the coastal Amsterdam Waterworks dune area near the village of Zandvoort, The Netherlands (longitude 05°11' E, latitude 52°06' N). Large amounts of surface water from the River Rhine (up to 150 million cubic meters year^{-1}) are infiltrated in this part of the sandy dune area, recharged in infiltration canals, and recollected from a central basin, Oranjekom, for further treatment preceding the use for drinking water purposes. The infiltration canals, with depths up to 2.5 m, host a large variety of aquatic plants. The current study has been carried out in the Western Canal part of the infiltration canal system (Table C1).

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[1] Unpublished report entitled, "Biomass Characteristics and Photosynthetic Activity of Sago Pondweed Populations in the Western Canal Near Zandvoort, The Netherlands" by E. P. H. Best, F. H. H. Jacobs, and H. Van de Hagen 1987.

Table C1
Properties of the Infiltration Canals in the Amsterdam Waterworks Dune Area, The Netherlands, in 1987
Water Quality Data, Mean Values (N=25)

Property	Value
All Canals	
Total estimated length (km)	30
Width (m)	35
Residence time[1] (d)	60-400
Maximum depth (m)	2.5
Western Canal	
Mean extinction coefficient (m^{-1})	1.07
pH	7.8-8.35
Mean total alkalinity (mg L^{-1})	182
Mean nitrate (mg L^{-1})	6.30
Mean total-phosphate (mg L^{-1})	0.112

[1] Time between intake from river and use as drinking water

Standing Crop

Plant biomass of sago pondweed was estimated by harvesting three squares in the middle of a plant bed at regular intervals during 1987, using SCUBA. Each time, three 0.25- by 0.25-m squares were harvested. Four depth classes were studied, i.e., rooting at 0.5, 1.0, 1.5 and 2.5 m. All biomass samples were rinsed thoroughly and dried at 105 °C until constant weight. Ash was determined by combustion of the organic matter at 440 °C. Biomass was expressed in g ash-free dry weight (AFDW) m^{-2}. The data on the 1.0-m rooting class were used for calibration of the POTAM model (Table C2).

Table C2
Standing Crop of Sago Pondweed in the Western Canal in 1987, Mean Values (N=3)

Day No.	Plant Biomass, g AFDW m^{-2}			
	0.5 m	1.0 m	1.5 m	2.5 m
98	0.09	0.64	0	0
134	0.22	8.00	4.02	0
190	12.75	50.00	65.19	
233	32.29	78.50	76.74	54.63
260		52.00		82.27
289	39.80	29.50	27.92	39.36
294	0	18.8	18.6	0
304	0	0	0	0

Plant Biomass Distribution over the Water Column

In the period when the vegetation reached peak biomass at the end of July 1987, five sago pondweed plants of the 1-m depth class were carefully excavated in such a way that the whole plants were kept intact. The plant samples were divided into 0.1-m layers from top to bottom, and the fresh and dry weights of the plant portions were determined as described previously.

The collected data (Table C3) indicated that plant biomass was contained for 91.4 percent in shoots and for 8.6 percent in roots. Most plant biomass was concentrated for >75 percent (78.4) in the upper 0.5 m of the water column and followed a typical vertical distribution over the water column. The same trend of concentrating biomass in the upper 0.5 m of the water column was observed in the other depth classes.

Table C3
Plant Biomass Distribution over the Water Column of Sago Pondweed in the Western Canal in July 1987, Mean Values (N=5)

Depth Layer from Water Surface	Biomass	
	Absolute, g AFDW m^{-2}	Relative, percent total
0-0.1	1.7	4.3
0.1-0.2	1.7	4.3
0.2-0.3	9.1	23.1
0.3-0.4	10.0	25.4
0.4-0.5	8.4	21.3
0.6-sediment	5.1	12.9
In sediment	3.4	8.6
Total	39.4	100

Species-characteristic Light Extinction Coefficient of Sago Pondweed

The species-specific light extinction coefficient of sago pondweed was determined as follows. Light readings were taken just above the water surface, just below the water surface, and further at 0.10-m intervals down the water column just outside and within a sago pondweed plant bed. The height of the vegetation within the water column was recorded, and five 0.04-m^2 vegetation squares were harvested. Samples were transported to the laboratory. The vegetation was cut into 0.10-m sections from just above the sediment to the top of the vegetation, coded appropriately, and dried at 105 °C for 24 hr to constant mass. Dry weights were determined to the nearest 0.01 g.

The light intensity at depth h (in m) from the upper surface of the plant community, designated by I_{z+h} may be approximated by the following Lambert-Beer's law:

$$I_{z+h} = I_z \exp(-\varepsilon_c h) = I_0 \exp(-\varepsilon_s z - \varepsilon_c h)$$

in which

$I_z =$ the light intensity on a horizontal plane at the upper surface of the plant community (μmol m^{-2} s^{-1})

$\varepsilon_c =$ the light extinction coefficient within the plant community (m^{-1})

$z =$ depth of the upper surface of the plant community, m

$I_0 =$ the light intensity passing through the water surface, approximated by the light intensity at 0.01-m depth under the water surface (μmol m^{-2} s^{-1})

$\varepsilon_s =$ the light extinction coefficient in the water outside the plant community (m^{-1})

The light extinction coefficient inside the plant community or ε_c represents the depth-dependent rate of light attenuation due to the absorption of light by both water and plant shoots. The light extinction coefficient due to the interception by shoots alone (ε_p in m^2 g^{-1} DW) was determined using the following equation

$$\varepsilon_p = (\varepsilon_c h - \varepsilon_s h) / w(h)$$

(C2)

in which w is the plant dry weight in g DW m^{-2}.

The measured data used to calculate the shoot-specific light extinction coefficient for sago pondweed have been summarized in Table C4. In all cases similar values were found varying from 0.084 to 0.107 m^2 g^{-1} AFDW . These values are far higher than reported by other investigators (0.0183 to 0.020 m^2 g^{-1} DW).

Table C4
Calculation of Species-Specific Light Extinction Coefficient for *Potamogeton pectinatus* Growing in the Western Canal

Replicate	I_z Water Column μmol m^{-2} s^{-1}	I_z Within Plant Community μmol m^{-2} s^{-1}	ε_s Water Water Column m^{-1}	ε_c Community Water and Plant Community m^{-1}	Cumulative Plant Biomass g DW m^{-2}	ε Plant Plant m^2 g AFDW^{-1}
Repl. 1						
0 m*	765	824			0	
0.1 m	731	735			0	
0.2 m	702	701			0	
0.3 m	708	523			1.84	
0.4 m	628	128			12.39	
0.5 m	606	40			26.48	
0.6 m	558	31	0.835	6.316	35.82	0.084
0.7 m	514					
0.8 m	478					
0.9 m	441					
						(Continued)

Note: I_z = light intensity at depth z; ε = light extinction coefficient; * = just below water surface.

Table C4 (Concluded)

Replicate	I_z Water Column μmol m^{-2} s^{-1}	I_z Within Plant Community μmol m^{-2} s^{-1}	ε_s Water Water Column m^{-1}	ε_c Community Water and Plant Community m^{-1}	Cumulative Plant Biomass g DW m^{-2}	ε Plant Plant m^2 g AFDW^{-1}
Repl. 2						
0 m	775	790				
0.1 m	720	758				
0.2 m	640	730				
0.3 m	584	473			0.94	
0.4 m	555	90			6.96	
0.5 m	581	65			18.359	
0.6 m	458	21			28.97	
0.7 m	514	9	0.835	6.351	35.82	0.093
Repl. 3						
0 m						
0.1 m		790				
0.2 m		753				
0.3 m		670			0.94	
0.4 m		382			6.96	
0.5 m		310			18.35	
0.6 m		126			28.97	
0.7 m		35	0.835	6.166	35.82	0.107
0.8 m		11				
Repl. 4						
0 m		794				
0.1 m		744				
0.2 m		690				
0.3 m		615			1.84	
0.4 m		530			12.39	
0.5 m		172			26.48	
0.6 m		140	0.835	4.618	35.82	0.088
0.7 m		22				
Repl. 5						
0 m		821			1.84	
0.1 m		747			12.39	
0.2 m		715			26.48	
0.3 m		664	0.835	5.083	35.82	0.089
0.4 m		221				
0.5 m		90				
0.6 m		66				
0.7 m		21				
Repl. 6						
0 m		1030				
0.1 m		974				
0.2 m		892				
0.3 m		417				
0.4 m		613				
0.5 m		215				
0.6 m		90			3.34	
0.7 m		56			22.33	
0.8 m		1	0.835	4.222	35.82	0.107
Mean						**0.095**

Seasonal Changes in Maximum Photosynthetic Activity at Light Saturation

Plant material

Sago pondweed tubers were collected in October 1987 in the Western Canal. These propagules were used to start a plant culture in 1.5-m-deep, 1-m-diameter, polyethylene containers, containing tap water and sediment from the Western Canal. The water was initially amended with bicarbonate up to 280 mg HCO_3 L^{-1} as inorganic carbon source. The culture was kept on the grounds of the Centre for Agrobiological Research (CABO), in Wageningen, The Netherlands.

Photosynthesis and respiration measurements

At regular intervals during 1987-1988, whole plants and tubers were harvested from this culture to determine their photosynthetic and respiratory activities using the standard Infra Red Gas Analysis (IRGA) Facility of the CABO, Wageningen, The Netherlands. All gas exchange measurements were performed in 500-mL Perspex vessels, containing 200 mL M-medium amended with 280 mg L^{-1} bicarbonate (added as $NaHCO_3$) and a pH of 7.0. Inflowing air was wetted prior to entering the vessels to prevent loss of medium during the incubation. Temperature was 20 °C, unless indicated otherwise. Each time individual plants were exposed successively to darkness and seven increasing light levels (15, 22, 30, 50, 62.5, 75 and 100 percent) up to 1121 μmol m^{-2} s^{-1} (270 W m^{-2}), measured just under the lid of the vessel equipped with a photocell). Successive light levels were changed when photosynthetic activity had stabilized. Light was provided by Philips 400 W HPIT metal halide lamps, and light levels were changed by changing the distance between lamp and vessel. Total duration of each incubation was usually 6-8 hr. Incubations were replicated four times. Before incubation, the plants were rinsed carefully with tap water to remove loosely attached periphyton, and their fresh weights were recorded. After incubation, dry weight, ash content, and the concentrations of starch and soluble sugars were determined.

Maximum Photosynthetic Rate at Light and CO_2 Saturation, and at Air Levels of CO_2

Maximum photosynthetic rates were far higher at light and CO_2 saturation than at air levels of CO_2 (Table C5).

| Day No. | Maximum Photosynthetic Rate at Light Saturation | | | |
| | CO$_2$-saturated (this study) | | Air Levels of CO$_2$ (Van der Bijl et al. 1989) | |
	Absolute g CO$_2$ g DW^{-1}h^{-1}	Relative (percent highest value)	Absolute g O$_2$ g DW^{-1} h^{-1}	Relative (percent highest value)
130			0.002	11
135			0.007	48
141			0.014	100
146	0.039	100		
156			0.013	93
162			0.009	65
178	0.028	73		
194	0.012	31		
209	0.023	58		
217			0.008	56
225	0.021	54		
227			0.008	59
244			0.008	59
250	0.025	65		
274			0.006	44
278			0.005	37
287	0.034	89		
291			0.003	24
294	0.025	64		
329	0.019	50		

Table C5
Maximum Photosynthetic Rates of Sago Pondweed Plants Incubated under Standard Laboratory Conditions, Using IRGA

Note: Plants originated from a culture started from tubers harvested from the 1-m depth class in the Western Canal. Mean values and SD (N=4). For comparison photosynthetic rates of sago pondweed measured in the field (freshwater River Susa, Denmark) using the oxygen exchange method are given.

Effect of Daytime Temperature on Photosynthesis (AMTMP)

To calibrate the relationship between temperature and photosynthetic activity, the photosynthetic rates relative to the rate at 30 °C found by the authors of this appendix (Table C6) were used. The very low values of 0.00001 have not been measured, but were assigned to photosynthetic activity at 0 and 50 °C.

Growth

The value of the conversion factor for growth of leaf biomass, weighted according to its composition, can be computed in a simple way from the fractions of nonstructural carbohydrates, proteins, fats, cellulose, organic acids, and minerals (Table C7). This conversion factor indicates the amount of glucose consumed to produce each g of leaf biomass (g CH$_2$O g DW^{-1}). This method has been employed to calculate assimilate requirements for biomass production of sago pondweed leaves.

Table C6
Relative Photosynthetic Activity of Sago Pondweed Shoots in Response to Temperature as Used for Calibration of the Model

Temperature, °C	Photosynthetic Rate	
	Absolute, g CO_2 g DW h^{-1}	Relative to Highest Value
0		0.00001
10	0.00440	0.027
18	0.00844	0.51
20	0.00881	0.53
23	0.01174	0.71
28	0.01505	0.91
30	0.01652	1.000
50		0.00001

Table C7
Estimated Chemical Composition of Sago Pondweed Shoots (this study), and Typical Conversion Efficiencies for Agricultural Crops, Showing How Much Glucose Is Used for the Synthesis of Each Organic Matter Component (Penning de Vries and Van Laar 1982b)

Component	Contribution to Biomass percent	Conversion Factor g CH_2O g DW^{-1}
Non-structural carbohydrates	20.5	1.242
Proteins	12.5	1.704
Fats	6	3.106
Cellulose	30	2.174
Organic acids	11.2	0.929
Minerals	16.8	0.050
Milfoil shoot	100	1.455

Note: As the conversion factor for cellulose was not known, that for lignin has been used.

Tuber Characteristics: Size, Carbohydrate Reserves, and Respiratory Activity

Size, carbohydrate reserves, and respiratory activity were determined in the sago pondweed tubers collected in October and subsequently kept in culture at the CABO grounds. Starch was measured in perchloric acid extracts of the plant material according to Hewitt (1958).[1] The soluble sugars were determined in hot water extracts using enzymatic techniques (Bergmeyer 1970). All determinations were done in triplicate. A detailed description of the latter procedure is given by Best and Visser (1987).

The average tuber size was 0.083 ± 0.012 g DW tuber^{-1} (N=12). The concentrations of starch ranged from 33.1 to 53.2 percent and those of soluble

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[1] References cited in this appendix are listed in the References section at the end of the main text.

sugars from 9.4 to 17.0 percent dry weight (Table C8). The respiratory activity, monitored on average over a period of 40 hr to allow respiration to reach steady state, was 0.003623 ± 0.0003 g CO_2 g DW^{-1} h^{-1} at 20 °C (N=12).

Table C8 Carbohydrate Reserves in Sago Pondweed Tubers Harvested in Autumn 1987 from the 1-m Depth Class in the Western Canal Mean values and SD (N=3)		
Day No.	Starch, % AFDW	Soluble Sugars % AFDW
82	33.1 ± 0	17.0 ± 0.5
285	38.8 ± 13.6	9.4 ± 1.1
331	53.2 ± 2.1	14.8 ± 0.7
346	46.1 ± 0.8	6.9 ± 0.3

Site-specific Environmental Conditions

pH, alkalinity, and trophic state are important factors influencing primary production in aquatic systems. pH and alkalinity determine carbon availability for photosynthesis, and trophic state gives an indication of algal production and consequent light attenuation within the water column. The model is calibrated for dissolved inorganic carbon concentrations around 2.5 mmol (Table C1).

pH affecting potential photosynthetic rate at light saturation through REDAM can be modified by the user.

The model is calibrated for a light-extinction coefficient range of the water of 0.82 to 1.974 m^{-1} (mean 1.07, Table C9); the value of this parameter (L) can be modified by the user.

Water Temperature

The temperature has been measured in the surface water of the Western Canal at several points in time in 1987 (Table C9). For days 1 and 365 the same temperatures as those measured on the nearest dates have been taken. Temperatures in all other canals were similar, but slightly higher in the Eastern Canal.

Table C9
Seasonally Measured Daytime Temperatures in the Surface Water of the Western Canal during 1987

Day No.	Temperature, °C	Light Extinction Coefficient, m^{-1}
7	5.5	0.845
14	Ice	
28	7.5	1.196
35	6.5	0.907
42	7.5	
49	6.0	
57	7.0	1.632
63	4.5	1.022
68	5.0	1.165
77	7.5	1.123
84	10.0	1.236
91	9.5	1.046
99	10.5	1.037
105	8.0	0.928
112	13.0	1.291
119	14.0	0.817
133	10.5	1.217
140	12.0	1.401
147	15.0	1.703
155	14.0	1.022
162	11.5	0.981
169	13.0	0.830
175	14.0	0.828
183	16.0	0.821
202		1.157
210	14.0	1.974
217	14.5	0.805
224	16.5	0.993
232	17.0	1.340
238	14.0	0.988
245	15.0	0.912
252	14.5	0.959
260	14.0	0.960
266	15.5	0.899
273	13.0	0.907
281	12.5	0.939
287	12.0	0.898
295	12.0	1.066
301	12.0	0.902
309	11.0	0.824
315	10.0	1.089

Appendix C   Manipulation of Literature Data Used for the Model Equations

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13. SUPPLEMENTARY NOTES

14. ABSTRACT

A simulation model for biomass dynamics of the submersed macrophyte *Potamogeton pectinatus* L. is presented. The model (POTAM) is based on carbon flow through the vegetation in meter-squared (m^2) water columns. It includes descriptions of several factors that affect biomass dynamics, such as site characteristic changes in climate, temperature, water transparency, water level, pH, and oxygen effects on CO_2 assimilation rate at light saturation, wintering strategies, mechanical control (removal of shoot biomass), and grazing. The characteristics of community and site can be easily modified by the user.

POTAM incorporates insight into the processes affecting the dynamics of a sago pondweed community in relatively shallow, hard water (0.1- to 6-m depth; dissolved inorganic carbon concentration > 0.8 mmol and pH > 6), under ample supply of nitrogen and phosphorus in a pest-, disease-, and competitor-free environment under the prevailing weather conditions. It has been calibrated on data pertaining to a sago pondweed community in the Western Canal near Zandvoort, The Netherlands. At this site, growth starts from the subterranean tubers alone. Plant biomass usually peaks once a year, in July, and intensive downward transport of soluble carbohydrates occurs after anthesis, used for the formation of tubers that grow into the sediment.

(Continued)

15. SUBJECT TERMS		
Biomass dynamics Carbon flow	Plant growth Potamogeton pectinatus Simulation model	

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14. ABSTRACT (continued)

POTAM simulated the dynamics of plant and tuber biomass and tuber numbers in the Western Canal near Zandvoort, The Netherlands, well over a period of 1 to 5 years. Starting from measured instead of nominal tuber size increased the similarity between simulated and measured plant data. The importance of several plant species-characteristic properties was explored, namely, of leaf surface:dry weight ratio, tuber bank density, anchorage depth, and presence/absence of wintering shoots.

The model has been used to calculate plant and tuber biomass and tuber numbers for other sites as well. In Lake Veluwe, The Netherlands, a site with a temperate climate, simulated plant biomass and newly produced tuber densities were similar to measured ones in two consecutive years, but timing in the simulated plants was delayed the second year. In the Byrnes Canal, California, with a far warmer temperate climate, simulated plant biomass and tuber bank density were similar to measured values when a lower self-shading coefficient than the nominal one and the same tuber size/tuber number per plant as measured were used. However, plant biomass and tuber bank density were lower with the nominal self-shading coefficient. In the tropical Lake Ramgarh, India, a simulated peak plant biomass similar to measured was found using the same lower self-shading coefficient as run for the California site, and almost no tubers were formed. Verification of simulated with measured tuber numbers was not possible, since tubers had not been measured.

Several case studies are presented in which POTAM generated insight useful for management aimed at conserving or controlling sago pondweed populations. The model was used to calculate the tentative effects on sago pondweed populations of (a) water level fluctuations, including floods and droughts, in the Upper Mississippi River; and (b) plant and tuber mass removal by cutting or grazing.

Sensitivity analysis showed that maximum plant biomass is most sensitive to a change in photosynthetic activity at light saturation but not to a change in light use efficiency. Maximum plant biomass was also strongly affected by changes in pre-anthesis development rate. End-of-year tuber number was sensitive to 7 out of the 9 parameters tested. Sensitivity was greatest to changes in pre-anthesis development rate.

Effects of changes in environmental factors were analyzed by applying the same method as used for sensitivity analysis. Maximum plant biomass and end-of-year tuber number proved to be sensitive to changes in climate.

The model can be used as a tool to predict the dynamics of a sago pondweed community over 1- to 5-year periods. Running the model with different parameter values specific for any particular site and/or treatment helps in gaining insight into the predominant mechanisms regulating submersed plant dynamics.